A STUDY OF THE VARIATION IN RESPONSE TO CLIMATIC STRESS WITHIN AND BETWEEN BREEDS OF SHEEP

by

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ABSTRACT

This thesis concerns an investigation of the ability of sheep to withstand cold. It includes studies of the initial cold resistance, the ability to acclimatize to cold, and of the variation within and between breeds of sheep. The cold resistance of shorn Scottish Blackface, Southdown and Welsh Mountain sheep, equal numbers on high or maintenance levels of nutrition, was measured by the rate of decline of rectal temperature under acute cold exposure (-20°C; 4 m.p.h. wind). Their ability to acclimatize to cold was determined by the effect of three types of cold exposure on subsequent cold resistance. These were; 2 weeks at a moderately subcritical temperature (+8°C), up to 8 hrs. acute exposure, or a combination of the two. Associated physiological responses such as changes in skin temperature, heart rate, respiration rate and skinfold thickness were also measured.

Cold resistance was greatest in the Blackface and least in the Welsh sheep. The mean rates of decline of rectal temperature were 0.636, 1.105 and 1.791 °C/100 min. exposure for Blackface, Southdown and Welsh sheep respectively. High plane sheep had greater cold resistance than low plane, but there was no evidence for interactions between breed and nutrition. There was considerable variation between individuals within breeds; coefficients of variation ranged from 25% to 66%. Individual repeatability of performance was high.

The cold resistance of all breeds was increased by previous exposure to +8°C, while an increase in cold resistance as a result of acute cold exposure alone was clearly shown by the Blackface sheep. These findings indicated that sheep could acclimatize to cold. Blackface sheep had a much greater capacity for acclimatization than either Southdown or Welsh

sheep. The mean rates of decline of rectal temperature were 74%, 19% and 32% slower respectively after acclimatization. In general both high and low plane sheep showed similar amounts of acclimatization. There was some inconclusive evidence for breed x nutritional interactions in ability to acclimatize.

It was concluded from indirect evidence and by analogy with previous work on rodents that acclimatization probably resulted from an enhanced capacity of the sheep to maintain high rates of metabolism under cold exposure, while in Blackface sheep a slight change in the site and efficiency of heat production involving a reduction in shivering thermogenesis may also have contributed.

Prolonged exposure to +8°C caused an elevation in rectal and skin temperatures and in heart rate when subsequently measured at a thermoneutral temperature. Rectal temperatures were, on average, 0.15°C higher, ear and foot temperatures 3.2°C and 2.5°C higher respectively, while heart rates increased by 40-50%. This evidence implied a considerable increase in the basal metabolic rate. Vasomotor responses under subsequent acute cold exposures were delayed. Vasoconstriction occurred, on average, 4°C and 7°C later respectively in the ears and feet. Acute cold exposure appeared to have a similar effect on basal metabolism.

Sheep kept at moderately sub-critical temperatures for long periods of time allowed, on average, a reduction in body temperature of 0.4°C. This was also shown during initial stages of acute cold exposure.

The increase in cold resistance and the associated responses appeared to have slightly different properties. Both were induced by prolonged exposure to +8°C or by acute cold exposure, but apparently only the increased resistance to body cooling was able to persist without continuous

low temperature stimulation.

Evidence for acclimatization was also found in new born lambs. Lambs born and reared for 2 weeks at 0°C maintained a rate of fall of rectal temperature 30% slower during acute cold exposure than comparable lambs which had been kept at +25°C.

The relevance of these findings to sheep in their natural environment and to climatic studies in the laboratory was discussed.

The vasomotor responses of Blackface, Southdown and Welsh sheep under mild cold exposure in full fleece were also compared. In general, estimates of the critical temperature, defined as the ambient temperature obtaining immediately after vasoconstriction of both extremities, were in good agreement with those of other workers who used calorimetric determinations. These were +1°C, +3°C and +7°C for the Blackface, Southdown and Welsh sheep respectively. Estimates for high plane sheep were generally 2°C lower than those for comparable low plane sheep. Southdown sheep, by comparison with the two hill breeds, appeared to have a rather low critical temperature relative to their fleece length, wool weight per unit area and bodyweight. This was thought to be due to their more comprehensive fleece cover on the face, ears and feet. It was suggested that vasomotor responses may be useful indices of variation in critical temperature within breeds but their validity in comparisons between breeds seems questionable when the sheep are unshorn.

CONTENTS

INTRODUCTION

The climate physiology of sheep has been extensively studied and reviewed (Hutchinson and Wodzicka 1961, Blaxter 1962, 1964). However the refined techniques used in such studies for the measurement of heat loss and insulation have, of necessity, restricted the work to small numbers of highly trained animals. Thus, while it is often claimed that some breeds of sheep are more suited than others to cold environments, the extent of variation within and between these breeds has never been assessed. Moreover, although some effects of nutrition on the responses of sheep to cold have been established (Blaxter, 1962), the possibility that breed x nutrition interactions may exist has not been investigated.

Considerable evidence has also been accumulated, especially in rodents (Hart, 1957, 1963) and to a lesser extent in man, suggesting that in mammals the recent thermal history may be a contributory factor to any variation which may exist between individuals in response to cold. A reduction in the deleterious effects of cold exposure, termed acclimatization, was ascribed to previous cold experience. No such evidence has yet been produced in sheep. Nevertheless any ability to acclimatize to cold would seem important to sheep in their natural environment, to physiologists making repeated studies on single animals, and to the geneticist who may wish to separate genetic and environmental components of variance.

This thesis describes experiments which were designed to investigate these problems. The first section concerns experiments which were carried out on shorn sheep to investigate whether breeds from different climatic regions differed in cold resistance and in ability to acclimatize to cold, and to assess possible breed x nutrition interactions in these characters. It soon became apparent that cold acclimatization was an important

phenomenon in sheep. Emphasis was therefore placed on this aspect of the work. The second section describes some responses of sheep to cold exposure in full fleece. Simple techniques were used throughout to permit comparisons of large numbers of animals.

REVIEW OF THE LITERATURE

Sheep, as homeotherms, maintain a relative constancy of body temperature despite fluctuations in the temperature of their environment. Within a certain range of environmental temperature, termed the 'thermoneutral zone', body temperature is maintained without change in heat production. The critical temperature marks the lower limit of the thermoneutral zone, and is the environmental temperature at which heat production must increase to prevent a fall in body temperature. In general, reactions towards a reduction of heat loss, e.g. postural changes, huddling - their effectiveness was demonstrated in pigs by Mount (1960, 1964b) - increased tissue insulation as a result of vasoconstriction (Blaxter, Graham, Wainman and Armstrong, 1959; Slee, 1964, 1966; Webster and Blaxter, 1966) and minimization of evaporation of water from the respiratory passages (Blaxter et al. 1959; Alexander and Brook, 1960), occur above the critical temperature.

The critical temperature of an animal is largely determined by its minimal heat production and its total insulation. Minimal heat production is influenced by many factors such as activity (Clapperton, 1964) and pregnancy (Graham 1964), but mainly by nutrition. Blaxter (1962) showed that the heat production of a sheep with a 5mm. fleece was respectively 850, 1250 and 1600 kcal/m^2/24 hrs. on fasting, maintenance and full feeding nutritional regimes, and the corresponding critical temperatures 31°C, 25°C and 18°C respectively. The total insulation depends mainly on the length of the fleece. Thus Ritzman and Benedict (1931) found the critical temperature of a sheep in full fleece to be 0°C while that of the shorn animal was 18°C. Armstrong, Blaxter, Clapperton, Graham and Wainman (1960)

showed that at the maintenance level of feeding critical temperature decreased from about 32°C to 9°C as fleece length increased from 5 to 40mm. and further decreased to 0°C between 40 and 120mm. fleece length.

Below the critical temperature heat loss generally increases at a constant rate which is inversely related to the total insulation (Kleiber, 1961; Blaxter, 1962). Periodic reductions in tissue insulation do, however, occur at sub-zero temperatures as a result of spontaneous increases in extremity blood flow (Webster and Blaxter, 1966; Slee, 1964, 1966).

Heat production is increased mainly by shivering and by increased voluntary muscle activity. Summit metabolism describes the maximum heat production attainable at normal body temperature without voluntary muscle activity (Gelineo, 1934). Hutchinson (1965-66) reported an eightfold increase in metabolism above the basal level during cold exposure of adult sheep. Alexander (1962) found the summit metabolic rates of lambs to be five times higher than basal levels. The total resistance of an animal to hypothermia will be determined by its insulation and by its ability to produce and maintain high rates of metabolism.

Variation in these basic characteristics occurs among many mammals as a result of (1) adaptation - where variation is largely genetically determined within and between species living in wide extremes of climate, (2) seasonal acclimatization - where variation within individuals is associated with annual rhythms of climate and (3) indoor acclimatization - changes induced within individuals by exposure to controlled temperatures in climatic rooms. In the case of indoor acclimatization the stimulus has invariably been low temperature exposure, but in adaptation and outdoor acclimatization many non-temperature stimuli may also have been involved. Data have been accumulated on all three aspects, with particular reference to rodents and man.

Comparisons between species adapted to arctic and tropical climates were made by Scholander, Hock, Walters, Johnson and Irving (1950). In general, arctic mammals were larger and possessed greater fur insulation, resulting in lower critical temperatures and a slower rate of increase of heat loss below the critical temperature. Thus the critical temperature for the arctic ground squirrel was +10°C, whereas that for the tropical jungle rat was +25°C, while the arctic fox did not increase heat production until -40°C.

Work on man, reviewed by Hammel (1964), has involved comparisons of genetic groups indigenous to cold climates with immigrant white controls. Physiological reactions to cold have ranged from the comparatively high metabolism of the Eskimo (Adams and Covino, 1958), to the reduced shivering, lower metabolism and body cooling response of the Australian Aborigine (Scholander, Hammel, Hart, Le Mesurier and Steen, 1958). On the other hand Wyndham et al. (1964) found that Bantu tribesmen, by comparison with white controls, allowed body temperature to cool while maintaining high metabolic rates when exposed, nude, to cold in climatic rooms. This they suggested indicated a lower tissue insulation in the tribesmen.

Seasonal acclimatization may involve increases in pelage insulation in winter, as observed in deer mice (Hart and Heroux, 1953), the white rat (Heroux, Depocas and Hart, 1959; Heroux, 1962), the red fox (Irving, Krog and Monson, 1955), and the hare (Hart, Pohl and Tener, 1965). Hart (1956) described seasonal changes in the insulation of pelts of a variety of mammals. The changes were greatest in the larger mammals. In summer the pelt insulations of the deer mouse and the black bear were 21% and 51% lower, respectively, than their maximal winter values. Metabolic changes have also been observed; for example, Hart and Heroux (1953, 1963) and Heroux (1962) noted a greater summit metabolic capacity in winter-caught compared to summer-

caught rats when cold exposed in the laboratory. In consequence, survival times at low temperatures were increased. Basal metabolism showed no consistent change.

Test conditions for man have varied widely and, perhaps as a result, conclusions have differed. Budd (1962) and Budd and Warhaft (1966) found that during a winter in Antarctica men developed an increased resistance to body cooling, which they attributed to increased tissue insulation. But more general findings after prolonged outdoor cold exposure have been of higher skin temperatures, probably the result of a decrease in tissue insulation (Carlson, Burns, Holmes and Webb, 1953; Scholander, Hammel, Lange, Andersen and Løyning, 1958). The latter workers measured the responses of men while sleeping and working lightly clothed for two months in the Norwegian mountains. Heat production, while sleeping, was elevated more in acclimatized than in non-acclimatized men. On the other hand Davis and Johnston (1961), who gave nude subjects twelve standard monthly cold exposures, found less cold-induced elevation of metabolism during the late winter and early spring months. Other workers, for example Adolph and Molnar (1946), have found no evidence for seasonal acclimatization in man.

Indoor acclimatization has been much more intensively studied, especially in rodents. Prolonged low temperature exposure has generally resulted in a reduction in their low temperature limits for survival or an increase in their survival times at specified low temperatures, compared with controls kept at thermoneutral temperatures. Acclimatization has invariably involved the capacity for higher or more prolonged maintenance of summit metabolic rates. Such changes have been observed in the white rat by Gelineo (1934), Sellers, Reichman and Thomas (1951), Cottle and Carlson (1954), Krog, Monson and Irving (1955), Depocas, Hart and Heroux (1957), Heroux (1963), in mice

by Hart (1953a), in rabbits by Blair, Dimitroff and Hingeley (1951), Heroux (1967) and in the squirrel by Adolph and Richmond (1956) and Pohl and Hart (1965). Unlike outdoor acclimatization, indoor acclimatization has generally caused basal metabolic rates to be elevated by between 15% and 60%. Evidence for changes in pelage insulation has been conflicting. Hart (1953b), Hart, Heroux and Depocas (1959) and Heroux (1963) found no change. Barnett (1959) found that whereas the total insulation of the pelt was greater in mice reared at -3°C than in similar animals reared at +21°C, due to increased hair growth, the insulation of the shaved skin had in fact decreased. Heroux (1959 and 1963) found an increased vascularity of the ears of rats, resulting in higher skin temperatures, while Desmarais and Dugal (1951) described a light peripheral vasodilatation also in the ears of rats after acclimatization. Other workers, for example Blair (1951) and Leblanc (1967) have demonstrated a lower incidence of frostbite in the ears and tails of acclimatized, as compared with non-acclimatized rats, when subsequently cold exposed.

Consistent changes in the responses of humans to cold after previous low temperature exposure have not been observed. Glaser (1950) and Glaser and Shephard (1963) found less reduction in extremity and mouth temperatures on successive days of cold exposure. Davis (1963) found little change in skin temperature during successive identical cold exposures but a gradual reduction in metabolic rate and in body temperature. Horvath, Freedman and Golden (1947), on the other hand, found no evidence for acclimatization. It is difficult to draw definite conclusions about any of the work on adaptation, outdoor, or indoor acclimatization in man because of the wide variety of responses shown. Much of this variation can probably be explained by differences in test conditions, nutritional and clothing habits and in the parameters used to measure acclimatization.

A reduction in shivering intensity coupled with an increased metabolic rate and increased resistance to body cooling is a common finding in rodents after acclimatization outdoors (Heroux, 1962) and indoors (Sellers, Scott, Thomas, 1954; Heroux, Hart and Depocas, 1956; Cottle and Carlson, 1956). Reduced shivering intensity has also been shown in men as a result of seasonal acclimatization (Davis and Johnston, 1961) and indoor acclimatization (Davis, 1963), although resistance to body cooling has not been tested. This work has led to the concepts of shivering and non-shivering thermogenesis, and to the conclusion that in cold acclimatized animals the cold-induced increase in heat production is predominantly of the latter type. The significance of these changes is considered to lie in an enhanced efficiency of utilization of energy for temperature regulation (Davis and Johnston, 1961).

The precise causes of these metabolic changes after cold exposure are not clear, but current evidence suggests that endocrine and cellular enzyme changes may be implicated (Depocas 1960, 1961; Hannon, 1963).

A valid criticism of most of the work described, especially in rodents, would be the ad libitum feeding regimes adopted. Although feed intake was generally not recorded there is evidence to suggest that it probably increased. For instance, Donhoffer and Vonotzky (1947) and Sellers, You and Moffat (1954) have observed considerable increases in the food intake of rodents on transfer to cold in the laboratory, while Durer and Hannon (1962) showed the food intake of Husky dogs in the Arctic to be 75% higher in winter than in summer. Changes in metabolism induced during acclimatization may therefore have been confounded with the effects of increased energy intake.

There is virtually no evidence for adaptation to cold in sheep. It is often supposed that British hill breeds possess a certain hardiness which

renders them well suited to cold climates. White (1931) and Doney (1955) have suggested that this hardiness must be regarded as a property of the fleece. In this regard Alexander (1958) found a smaller heat loss in lambs with hairy birthcoats when subjected to wind and rain, while a relationship between weight loss over winter and fleece length, weight and fibre density has been shown by Doney (1963). Differences in tissue insulation between hill and down breeds of sheep were reported by Joyce (1964), but more recent work (Webster and Blaxter, 1966) has not confirmed this. Vasomotor responses in Blackface sheep were shown to be elicited at higher ambient temperatures than in Merinos (Slee, 1964) but this difference may have been related to fleece cover.

Acclimatization to cold has never been studied in sheep. Seasonal changes in wool growth are known to occur, but these are influenced by nutritional and daylight factors (Ferguson, Carter and Hardy, 1949; Hutchinson and Wodzicka, 1961; Morris, 1961) and wool growth is in fact depressed by cold (Doney and Griffiths, 1967). Moreover, normal husbandry practices ensure that fleece insulation is greatest in late winter. An increased skinfold thickness was observed in sheep after shearing (Wodzicka, 1958) and after cold exposure (Wodzicka-Tomaszewska, 1960a) but was not related to a change in insulation. These latter sheep (Wodzicka-Tomaszewska, 1960a) shivered continually immediately after shearing, but only intermittently some days later.

Seasonal changes in the heat tolerance of shorn sheep, measured by the rise in body temperature on heat exposure, have been observed, e.g. Wodzicka (1960b). Heat tolerance was greater in summer than in winter. Moreover, there is evidence in cattle for acclimatization to heat, e.g. Bianca (1959); Kibler, Johnson, Shanklin and Hahn (1965), probably involving a lowering of

basal metabolism.

Adaptation and various forms of acclimatization to cold are therefore well established phenomena in mammals, but the scant evidence for adaptation and the absence of evidence for acclimatization to cold in sheep, made the effects of low temperature exposure on sheep a worthwhile subject for study.

SECTION A. THE COLD RESISTANCE AND ACCLIMATIZATION OF SHEEP TO COLD

This section will deal with the cold resistance and ability to acclimatize to cold of three breeds of sheep.

MATERIALS AND METHODS

Scottish Blackface, Southdown and Welsh Mountain sheep were chosen for this study because of their wide distribution with respect to climate and environment. Forty-eight Scottish Blackfaces were used. Twenty-nine came from an A.B.R.O. hill farm in Peeblesshire; of these 14 were from a group of sheep selected since 1955 for high fleece medullation and 15 from a corresponding low medullation group (Pilkington and Purser, 1958 and Purser, 1967). The remaining 19 were similar but drawn from a random bred flock on a lowland farm in Midlothian. Thirty Southdown from a pedigreed flock in Sussex, and 30 Welsh Mountain from an A.B.R.O. hill farm in Montgomeryshire were also used. Ewe lambs, all eight months old at the commencement of treatment, were used throughout to minimise any effects of age or winter cold experience on performance. Southdowns were chosen as the 'down' breed because of their similarity in average bodyweight to the hill breeds.

Although desirable, it was impossible because of the large numbers of sheep involved, to undertake a high degree of training to experimental procedures. Prior to each experiment the sheep had 2-3 months in which to become accustomed to indoor feeding and regular handling, and each spent 1 day in the climate chamber (see Section B). Because all the experiments were to be of a comparative nature, this was considered acceptable. Some data on the effects of emotional disturbance are presented.

In addition, large numbers of sheep precluded elaborate techniques for the measurement of heat production and insulation. Related parameters were therefore measured. Thus heart rate, shivering intensity and respiration rate were used as parameters related to heat production, and skin temperature as a parameter related to insulation. Heart rate is not a satisfactory absolute measure of metabolic rate, being sensitive to many emotional as well as physiological factors. However, on the basis of current evidence it seemed reasonable to conclude that under standard conditions changes in heart rate would be indicative of synchronous changes in metabolic rate within animals. Blaxter (1948) found that the heart rate and metabolic rate of an individual sheep were highly correlated over a twofold range of heat production ($r = +0.930$), and more recently Webster (1967) demonstrated a good relationship over a small range of heat production. A good relationship has also been reported in cattle by Kibler and Brody (1949), Blaxter and Wood (1951) and by Roy, Huffman and Reineke (1957). In men, Swift (1932) and Glickman, Mitchell, Keeton and Lambert (1967), demonstrated a high correlation between shivering intensity and heat production under cold exposure.

The primary concern was to establish a standard technique of cold exposure which would show variation in response between individuals and could at the same time be used to test for acclimatization. The rate of decline of rectal temperature under acute sub-zero cold exposure was therefore used as a measure of the cold resistance of sheep. Vasomotor responses, changes in heart rate and the onset of shivering during a controlled lowering of ambient temperature from a thermoneutral to a subcritical temperature were also measured. Acclimatization was determined by the changes in cold resistance after prolonged cold exposure. The ambient temperature used to induce acclimatization was chosen by reference to previous work on rodents

and the findings of Armstrong et al. (1960) for the critical temperatures of shorn sheep. In attempting to induce acclimatization, the problem was to choose an ambient temperature which was sufficiently below the critical temperature to provide a stimulus while not so severe as to induce debility. Two weeks exposure to +8°C was therefore used. Previous work on rodents suggested that this would be a sufficient length of time for the induction of acclimatization.

Shorn sheep were used for two reasons, firstly so that sufficient cooling power could be imposed in order to lower body temperature within a reasonable time, and secondly because between individuals the fleece presents a variable and unknown resistance to body cooling.

Two fixed planes of nutrition were adopted, so that possible breed x nutrition interactions in resistance to cooling and ability to acclimatize to cold could be investigated, and to avoid confounding the effects of increased feed intake and acclimatization.

The experimental work is presented in two parts: (1) that on Blackface sheep carried out in 1965-66 and (2) that on Southdown and Welsh sheep in 1966-67. The results of a similar experiment on newborn lambs are presented in a third part.

PART ONE - SCOTTISH BLACKFACE SHEEP

EXPERIMENTAL PROCEDURE

The sheep were brought indoors on October 25th 1965 and gradually introduced to a standard* high fibre pelleted ration. On November 8th 32 sheep were equally divided into groups for high and low plane nutrition and subsequent temperature treatment, so that between groups there was an equal distribution with respect to farm of origin, fleece selection type and bodyweight (see page 11). The basic low and high plane rations were 23 and 36 gm./kg. bodyweight/head/day respectively, calculated from individual bodyweights on November 8th. While the low plane ration remained constant throughout, the daily high plane ration was increased each week by 30 gm./head until the beginning of temperature treatment, when it was stabilized. The low and high plane sheep were then consuming on average 630 gm./day and 1,300 gm./day respectively. These respective levels were chosen on the basis of past experience as capable of maintaining bodyweight and allowing a moderate gain in bodyweight.

Thirty-two sheep were subjected, between January and May 1966, to a series of double cold exposures. The day before the first cold exposure (day 1) each sheep was closely clipped to leave approximately 3-4 mm. of wool. Immediately after clipping and before 5 p.m. the sheep entered the climate chambers, where environmental temperature was +30°C (estimated as thermoneutral for the shorn sheep from the data of Blaxter et al. 1959, and Armstrong et al. 1960). They were loose-haltered in crates which permitted considerable freedom of movement but prevented the animals from turning round. Next morning (day 2) at 08.00 hrs. the sheep were yoked by the

*The composition is given in Appendix 1.

neck in a standing position. A metal bar was fixed under the belly to prevent the sheep from lying, while another was fixed just above the midback to prevent excessive movement. Equipment for the measurement of rectal temperature, skin temperatures at three sites - left ear, left midside and left foot (on the lower pastern just proximal to the hoof) - heart rate, muscle activity and respiration rate, was fitted by 09.00 hrs. Recordings commenced at 09.30 hrs. Room temperature was maintained at +30°C until 10.30 hrs. The sheep had then been allowed at least 17 hours to adjust emotionally and physiologically to the new environment, and 90 minutes for any effects of handling to subside. At 10.30 hrs. a controlled stepwise decrease in room temperature at a rate of 1°C/5 min. began. This continued for $2\frac{1}{2}$ hrs. until room temperature reached 0°C at 13.00 hrs. Then small individual fans, providing a 4 m.p.h. wind at the right midside of each sheep, were switched on and room temperature was lowered rapidly to reach -12°C at 13.30 hrs., -15°C at 14.00 hrs., -18°C at 15.00 hrs., and -20°C at 17.00 hrs. Individual exposures were terminated after 8 hrs. exposure from 13.00 hrs. or when rectal temperature had fallen to 37.5°C. After this acute cold exposure the sheep received one of two alternative treatments. One group spent the next two weeks at +30°C (these are subsequently referred to as HP30 and LP30 sheep), those in the other treatment group were first allowed to recover for 12 hours at +20°C and then remained at +8°C for two weeks (HP8 and LP8). On day 15 at 14.30 hrs. room temperature for the HP8 and LP8 groups was raised to +30°C. On day 16 all sheep were subjected to a second identical cold exposure, the HP8 and LP8 sheep having then had 18 hrs. to re-equilibrate to the newly-imposed thermo-neutral environment. Performance at the second cold exposure would therefore test for acclimatization to two types of cold experience, the acute

exposure and acute exposure supplemented by chronic exposure at +8°C. Eight sheep (2 in each treatment group) experienced slightly less severe, though identical, acute cold exposures due to refrigeration difficulties. Data from these sheep are included in all calculations except those in Fig. 1. The same series of experimental measurements were made at the beginning and end of the constant temperature periods (on days 4 and 14) from 10.30 to 14.30 hrs. on each day, as during the cold exposure days (2 and 16).

The sheep were reclipped closely on days 11 and 15. All sheep received maintenance rations on days 1 and 15, no food on days 2 and 16 until after cold exposure and $\frac{1}{2}$ maintenance rations on days 4 and 14 made up to full rations after measurements. On the other intervening days between acute cold exposures, normal high and low plane rations were fed. The intention was to maintain the established high and low plane differential, while attempting to minimise variation in post prandial heat increment due to large differences in food consumption on days when physiological measurements were made. Sheep were treated in pairs of quartets (one quartet on each temperature treatment). Each quartet comprised 2 high and 2 low plane sheep. Acute cold exposures for the pairs of quartets occurred on consecutive days so that any seasonal or age effects would be equalized between treatment groups. The basic experimental plan is presented in Table 1.

A further 8 sheep (4 high plane and 4 low plane) were shorn and spent two weeks in the climate chambers at +30°C before receiving their first cold exposure. The intention here was to test whether performance under the second acute cold exposure of the previous 4 groups of sheep could have been influenced by habituation to the climate chamber environment. These

Table 1. Experimental Plan

Treatment Groups	n	Day 1	Day 2	Day 4	Days 3-15	Day 14	Day 15	Day 16
HP30	8	Entered chambers at +30°C	1st acute cold exposure	1st Constant temperature measurement	kept at +30°C	2nd Constant temperature measurement	Chamber temperature raised to +30°C	2nd acute cold exposure
HP8	8	"		"	days 3-14 kept at +8°C	"		"
LP8	8	"		"	days 3-15 kept at +30°C	"		"
Feeding		Maintenance (↑ Shorn)	Fasted	½ maintenance	Normal ration (↑ Reshorn)	½ maintenance	Maintenance (↑ Reshorn)	Fasted

sheep, the habituation controls, were treated according to the normal procedure from the time of the first exposure onwards, and data derived from them was used in the main analysis. Finally the remaining 8 sheep (6 on high plane and 2 on low plane) were clipped and spent 2 weeks at +8°C before the first acute cold exposure. It was hoped that this treatment would give some indication as to whether performance under acute cold exposure could be influenced by chronic moderate cold exposure alone.

Rectal temperature was measured by copper-constantan 32 swg thermocouples inside 1/4" diameter polyethylene tubing inserted 13 cm. into the rectum, and secured by elastic tape to small tufts of wool on each side of the anus. Skin temperature was measured by copper-constantan 32 s.w.g. thermocouples cemented to closely-clipped skin under small pieces of 'Elastoplast'. The thermocouples were connected to a Honeywell-Brown 16 channel potentiometer which recorded at 5 min. intervals.

Heart rates were measured by electrocardiography (ECG) using needle electrodes attached to the chest wall. They were counted on an audible relay confirmed by oscilloscope display. During acute cold exposures counts proceeded over ½ min. periods at 15 min. intervals from 10.30 - 14.00 hrs. and subsequently at hourly intervals; and at hourly intervals from 10.30 hrs. on days 4 and 14 between acute cold exposures. At the same times shivering intensity was estimated from the activity of the pectoral and biceps femoris muscles, utilizing the same ECG electrodes on the chest wall and similar electrodes on the britch. It was estimated visually by assessing the mean and maximum oscilloscope trace amplitudes over observation periods of about 1 min. These amplitudes were then converted into millivolts. Gross estimates of shivering were also obtained by direct observation. Respiration rates were obtained from a thoracic belt fastened over the

penultimate rib, and connected through a tambour to a kymograph. During acute cold exposure, recordings were made for ½ min. periods every 30 min. from 10.30 hrs. until 15.00 hrs. and subsequently at hourly intervals. Hourly recordings were made on days 4 and 14 between acute cold exposures.

Sheep were weighed after shearing on days 1 and 15 (main treatment groups) and on days 1, 14 and 29 for the additional treatment groups. At the same times skinfold thickness was obtained as the mean of two skin pinches taken at right angles to each other on the right midside just posterior to the last rib. Harpenden spring calipers were used.

The air humidity in the climate chamber was not controlled but was recorded throughout the experiment. At any given ambient temperature little variation was encountered and this did not appear to influence any of the characters measured. At +30°C and +8°C the relative humidity of the air was approximately 40% and 70% respectively. At sub-zero temperatures the air would always be fully saturated. No further reference to humidity is considered necessary. There was no detectable variation in air movement or ambient temperature between the four animal crates in the chamber, but sheep in the different treatment groups were randomly allocated to crates. With the exception of the later stages of acute cold exposure when the small fans were operating, air movement at sheep height was, in fact, too small to be measured by a vane anemometer.

Statistical differences were calculated by t tests on paired differences within individuals where possible, or by conventional t tests, and by analysis of variance. In the tables means are presented with one standard error unit.

The term 'performance' in the text refers to the rate of decline of

rectal temperature during acute cold exposure. Good or improved 'performance' indicates a low or decreased rate of decline of rectal temperature under cold exposure.

RESULTS

MAIN TREATMENT GROUPS

There were no significant differences in performance between the sheep from different farms or those previously selected for differences in fleece type. Data from those classes of sheep have therefore been pooled. The responses of sheep just prior to and during acute cold exposures (days 2 and 16) are considered separately from those occurring between acute cold exposures (days 4 and 14) when the sheep were exposed to +8°C or +30°C.

1. Rectal temperature

a) During acute cold exposure (days 2 and 16)

The changes in mean rectal temperature for the four main treatment groups during first and second cold exposures are shown in Fig. 1. At +30°C ambient temperature, before the first cold exposure commenced, there were no differences between treatment groups in mean rectal temperature. However, under the same conditions before the second cold exposure, rectal temperatures of sheep kept at +8°C (HP8 and LP8 groups) were 0.23°C ($P < 0.01$) higher than those of sheep kept at +30°C (HP30 and LP30 groups). During first exposure all sheep showed a slight fall in rectal temperature as ambient temperature fell from +30 to +15°C followed by a gradual rise between +15°C and 0°C. During second exposure the HP30 and LP30 sheep showed similar changes in rectal temperature at these ambient temperatures. Rectal temperature of the HP8 and LP8 sheep, however, showed a much more pronounced decline as ambient temperature fell from +30°C, and at 0°C were 0.49°C ($P < 0.01$) and 0.44°C (N.S.) lower respectively on second than on first exposure. These sheep had apparently developed a cooling response

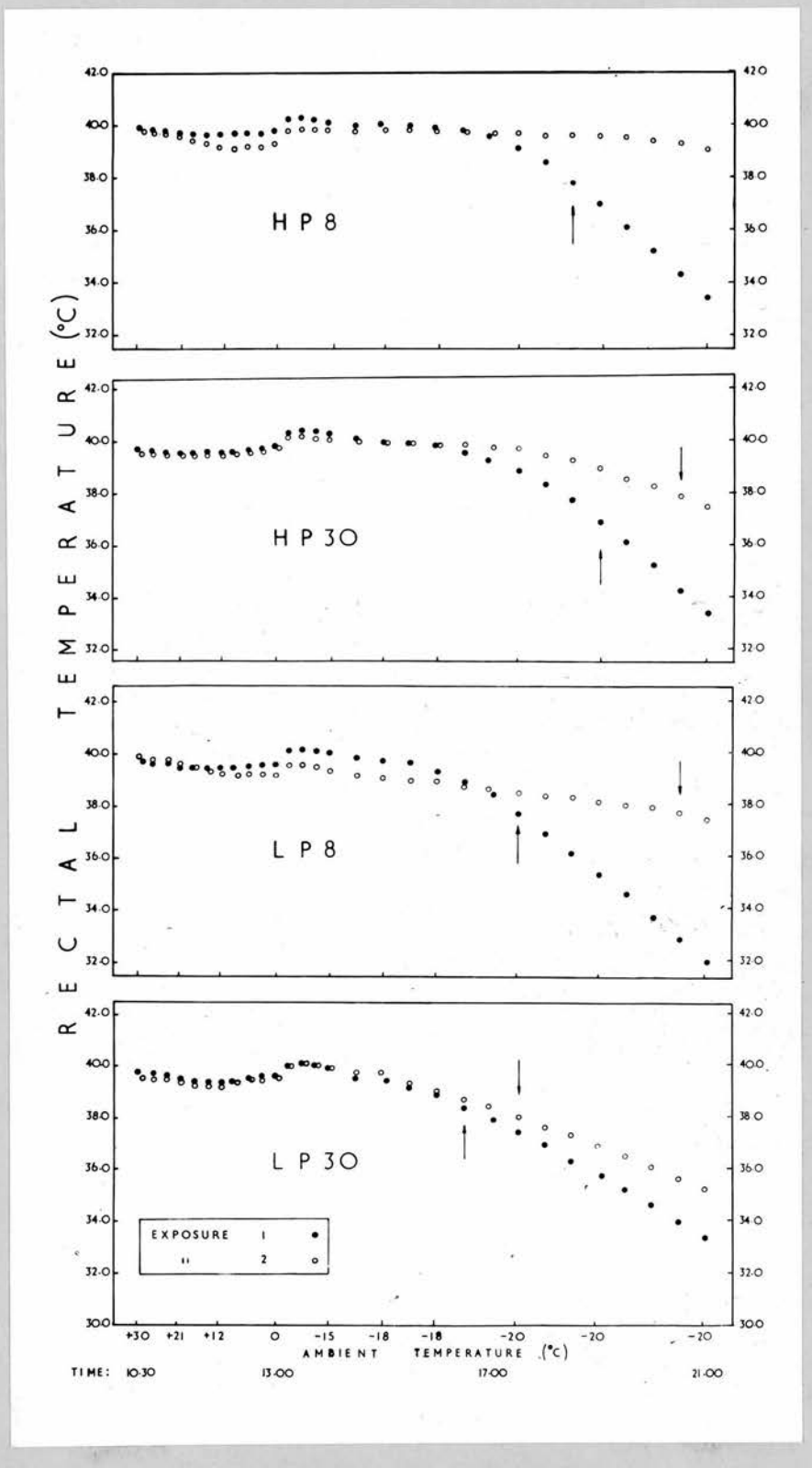


Fig. 1. The changes in mean rectal temperature in the four main treatment groups during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown. Arrows indicate the point on each line where extrapolation became necessary for two or more sheep per group.

to moderately subcritical temperatures, after prolonged exposure to +8°C.

The immediate response of all sheep to the rapid fall in ambient temperature introduced from 0°C was a rise in rectal temperature which reached a peak within 30 min. There was considerable variation between individuals in the extent of this rise. There were no significant differences attributable to treatment, though the rise tended to be more pronounced in high plane sheep.

Soon after low environmental temperatures were obtained the rectal temperatures of some sheep began to fall. Some reached the lowest permitted temperature (37.5°C) within three hours, whereupon the sheep were removed from the chamber. Other sheep showed little decline in rectal temperature after the maximum permitted exposure time (8 hrs.). In order to compare graphically the progressive changes in group mean rectal temperatures, individual values for those sheep removed from the chamber on cooling to 37.5°C were extrapolated to the maximum exposure time. The extrapolation was calculated on the basis of the rates of fall of individual rectal temperatures in the final 30 min. of exposure. This was considered justifiable for comparative purposes on the evidence of Slee (1966) and Slee and Wiener (unpublished) which showed, under similar experimental conditions, that rectal temperature once depressed below 38°C continued to fall at a steady or slightly increasing rate. Arrows on Fig. 1 indicate the point from which the mean involves extrapolated data from more than two individuals. The main conclusion is that all groups of sheep, especially those kept at +8°C between exposures showed a marked improvement in performance during second cold exposure.

Resistance to cooling increased because normal rectal temperatures were sustained for longer and rectal temperature subsequently fell less

rapidly. Table 2, in which performance is classified into three categories, shows that the increased ability to maintain rectal temperature resulted from: (a) a greater number of sheep showing no decline, or less than the maximum permitted decline on second exposure ($\chi^2 = 24.14$; $P < 0.001$), and (b) the much slower terminal rates of body cooling of all groups of sheep ($P < 0.001$ over all treatment groups). This effect was also significant ($P < 0.02$) even when only sheep showing the maximum permitted fall in both occasions were compared. On the other hand, high plane sheep, which were able to maintain normal body temperature longer and therefore had slower overall rates of cooling than low plane sheep, showed faster terminal rates of cooling than low plane sheep ($P < 0.001$ - all treatment groups combined).

For comparative purposes, performance was quantified by calculating the rate of decline of rectal temperature per 100 min. exposure from 0°C - Table 3a. Thus it was possible to compare directly sheep whose exposure was terminated when rectal temperature had fallen to 37.5°C with those showing little or no depression at the end of exposure. The disproportionately large improvement in performance shown by the HP8 sheep occurred because some sheep actually had higher rectal temperatures at the end than at the beginning of their second exposures. Presumably this reflected greatly increased metabolic or insulative capabilities. To some extent it must represent a threshold effect such that longer exposure periods, if used, would eventually have induced proportionately greater increments of temperature decline in sheep which were most resistant on the present scale.

Analysis of variance, Table 3b, showed that exposure occasion (i.e. whether first or second) and plane of nutrition had most influence on performance. Apparently the short acute cold experience during first cold exposure had more effect on subsequent performance than the prolonged period

Table 2.

Performance classification and terminal rates of cooling

Mean decline in rectal temperature during final $\frac{1}{2}$ hr. of exposure ($^{\circ}$C) and number of sheep involved (n).

Treatment group		Performance category						4 Maximum decline to 37.5°C on both 1st and 2nd exposures	
		1 No temperature decline		2 Decline less than maximum allowed		3 Maximum decline to 37.5°C			
		n	Mean terminal decline	n	Mean terminal decline	n	Mean terminal decline	n	Mean terminal decline
HP8	1st exposure	0	-	3	0.40	7	1.06	1	1.50
	2nd exposure	2	0.00	7	0.13	1	0.80		0.80
HP30	1st exposure	1	0.00	2	0.25	7	1.10	3	1.20
	2nd exposure	2	0.00	5	0.04	3	0.83		0.83
LP8	1st exposure	0	-	0	-	10	0.77	5	0.88
	2nd exposure	1	0.00	4	0.17	5	0.44		0.44
LP30	1st exposure	1	0.00	0	-	9	0.68	6	0.63
	2nd exposure	1	0.00	3	0.30	6	0.53		0.53

Table 3. Resistance to Cooling

a) Mean rate of decline of rectal temperature in main treatment groups

b) Analysis of variance

(a)

Treatment group	n	Rate of decline (°C/100 min. exposure below 0°C) 1st Exposure	2nd exposure	Signif. of diff. between 1st & 2nd exposures (P)	Rate of decline of rectal temperature at 2nd compared to 1st exposure (%)
HP8	10	0.544 ± 0.093	0.012 ± 0.055	<0.001	2.2
HP30	10	0.492 ± 0.141	0.232 ± 0.102	<0.01	47.1
LP8	10	0.771 ± 0.070	0.322 ± 0.108	<0.01	41.7
LP30	10	0.737 ± 0.134	0.510 ± 0.123	<0.02	69.1

(b)

Source of Variation	df.	M.S.	F	P
Nutrition	1	1.602	12.92	<0.001
Occasion of Exposure	1	2.438	19.60	<0.001
Temperature between Exposures	1	0.078	0.63	N.S.
Nutrition x Temperature	1	0.004	0.03	"
Nutrition x Occasion	1	0.002	0.02	"
Temperature x Occasion	1	0.399	3.15	"
P x T x O	1	0.019	0.02	"
Error	72	0.124		

of moderate cold between exposures; or the effect of acute exposure was sufficiently large to mask any due to moderate cold treatment. The large but non-significant interaction between temperature and occasion of exposure suggests that moderate cold exposure (+8°C) did have some influence on subsequent performance. The effect of previous cold experience was apparently greater than that of plane of nutrition; they accounted for 18% and 12% respectively of the total variation in performance.

To obtain some information on the retention of acclimatization, twelve sheep, approximately equal numbers from each treatment group, were kept in the chambers at +30°C for a further 2 weeks after their second acute cold exposure. They then received a third identical acute cold exposure. The mean rates of decline of rectal temperature were as follows: 1st exposure 0.728 ± 0.131; 2nd exposure 0.296 ± 0.126; 3rd exposure 0.324 ± 0.070. Most sheep showed a slight deterioration in performance from the second to the third exposure but the mean difference was not significant. Sheep showing a large improvement from first to second exposure tended to show most deterioration from second to third exposure and vice versa. The mean difference between both first and second, and first and third exposures were highly significant ($P < 0.001$ and $P < 0.01$ respectively).

(b) Between acute cold exposures (days 4 and 14)

Fig. 2 shows mean rectal temperature for the four main treatment groups on four occasions: after the sheep had remained undisturbed for 1½ hrs. at +30°C before the first cold exposure (i.e. on days 2 and 16 respectively) and on days 4 and 14 between acute exposures, at the treatment temperatures of +30°C and +8°C. As stated previously, there were no significant differences between group mean rectal temperatures on day 1. Analysis of variance on the data from days 4 and 14 showed that ambient temperature accounted for 18%

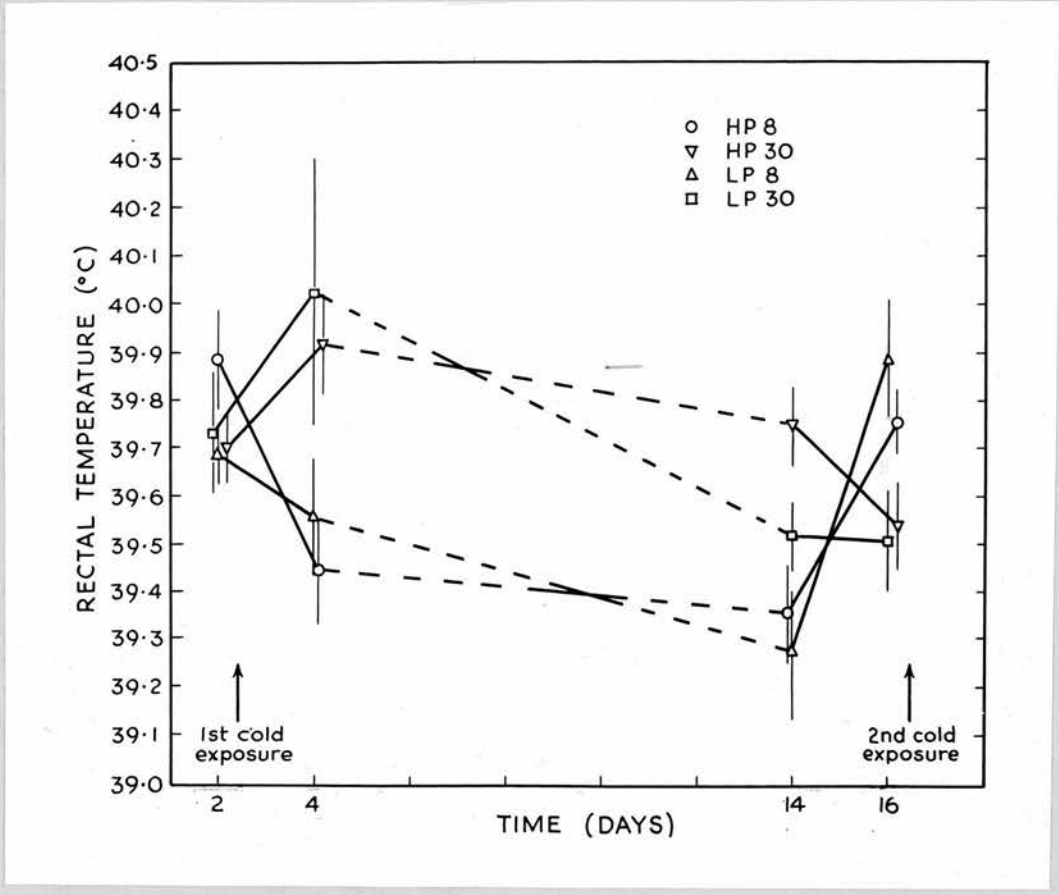


Fig. 2 Mean rectal temperatures in the four main treatment groups (10 sheep per group) before and between acute cold exposures.

On days 2 and 16 the ambient temperature was +30°C for all sheep; on days 4 and 14 the ambient temperatures were +8°C and +30°C according to the temperature treatment between acute exposures.

($P < 0.001$) and the two exposure occasions for 8% ($P < 0.01$) of the total variation in rectal temperature, while plane of nutrition had no effect. The data for different nutritional planes were therefore combined. Rectal temperatures of the HP30 and LP30 sheep were higher ($P < 0.05$) on day 4 than on day 1, whereas those of the HP8 and LP8 sheep had fallen ($P < 0.01$) in the same period, the difference between +30 and +8 sheep on day 4 being 0.45°C ($P < 0.01$). The rectal temperatures of both the +30 and +8 sheep showed similar and significant decreases between days 4 and 14 ($P < 0.02$ and $P < 0.05$ respectively). The difference in rectal temperature between the +30 and +8 sheep on day 14 was 0.32°C ($P < 0.001$). When the +8 sheep were returned to +30°C before the second cold exposure (day 16) rectal temperatures increased by 0.54°C ($P < 0.001$) from day 14, and were higher ($P < 0.01$) than those of the +30 sheep. Apparently, therefore significant changes in rectal temperatures resulted from differences in both the prevailing ambient temperature and the previous thermal environment.

(c) Emotional effects

The changes in rectal temperature of sheep at +30°C between 10.30 hrs. and 14.30 hrs. on days 4 and 14 provide an estimate of the duration of emotional disturbances caused during the fixing of equipment between 08.00 - 09.00 hrs. and possible diurnal variation in rectal temperature. In general rectal temperatures fell slowly between 09.00 - 10.00 hrs. but by 10.30 hrs. had reached a steady level. Between 10.30 hrs. and 12.30 hrs. rectal temperature fell on average by 0.2°C. The slight fall in rectal temperature shown by all treatment groups between +30°C and +15°C on first acute cold exposure and by the HP30 and LP30 groups of sheep on second exposure may therefore have been due to a decay of emotional disturbance associated with previous handling, coupled with possible diurnal changes.

(d) Variation in Performance

There was considerable variation in cold resistance at the initial exposure, ranging from a rectal temperature change during exposure of +0.031 to -1.379°C/100 min. on high plane ($\bar{x}$ = -0.585; C.V. = 66%), and from 0.054 to -1.420°C/100 min. exposure on low plane nutrition ($\bar{x}$ = -0.754; C.V. = 44%). There was also considerable variation in the extent to which the performance of sheep improved, especially those kept at +8°C. For example, in the HP8 group, one sheep showing a rate of fall of 0.542°C/100 min. on first exposure, actually had an elevated rectal temperature after the second cold exposure; whereas another in the same group had an initial rate of fall of 0.779°C/100 min. which was only reduced to 0.423°C/100 min. The most improved LP8 sheep showed a rate of fall reduction from 0.721 to 0.066°C/100 min., whereas the performance of two sheep actually deteriorated at second exposure. Individual repeatability of performance under cold exposure was quite high for the HP30 and LP30 sheep (r = +0.87, $P < 0.001$, and r = +0.82, $P < 0.01$ respectively); but was much lower for the HP8 and LP8 sheep (r = +0.54 (N.S.) and r = +0.35 (N.S.) respectively). Apparently, acute cold treatment caused a relatively uniform improvement in performance, whereas the addition of chronic moderate cold treatment produced a more varied response.

2. Skin temperature

(a) During acute cold exposure

The changes in mean midside, ear and foot temperatures during first and second acute cold exposures are shown in Fig. 3. There was no difference in midside temperature between groups of sheep during either exposure; they fell on average at a rate of 0.35°C/°C fall in ambient temperature when calculated over all treatment groups at both exposures. Rates of fall in individual sheep however varied from 0.15°C to 0.55°C/°C. No consistent evidence was

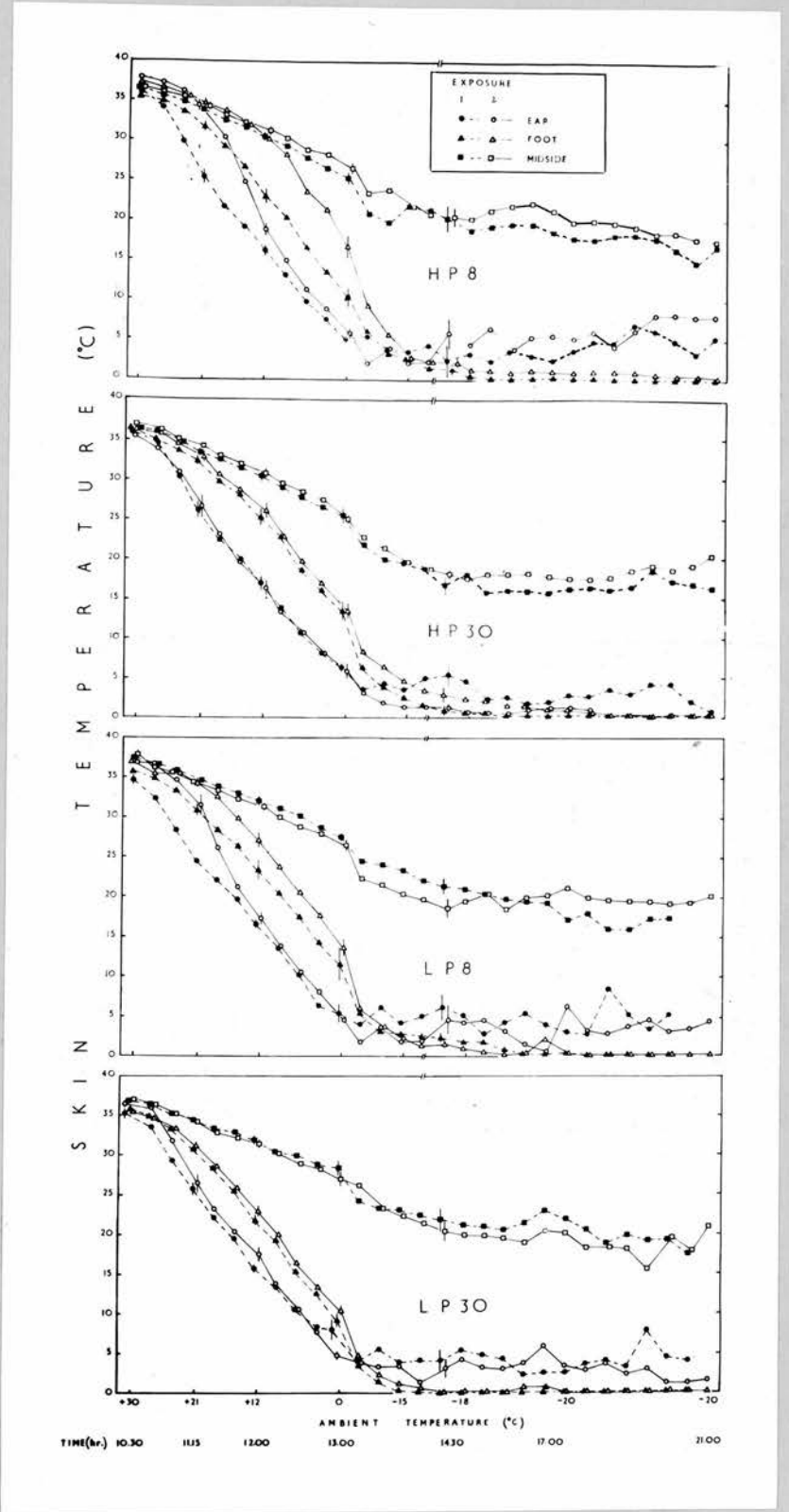


Fig. 3 The changes in mean midside, ear and foot temperature in the four main treatment groups (10 sheep per group) during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown. Standard errors are denoted by vertical lines. At +30°C they were too small to show on this scale.

found to suggest that the midside was capable of vasomotor responses, though at sub-zero temperatures occasional fluctuations did occur in a few sheep. There was no relationship between performance and midside temperature during exposure.

At ambient temperatures between +29°C and +21°C on the first exposure vasoconstriction occurred in the ears, and ear temperature fell rapidly until approximately 5-6°C above ambient temperature. At 0°C ambient temperature average ear temperature (all groups of sheep combined) was 5.5 ± 0.63°C. Foot temperatures showed a similar trend but the ambient temperature at vasoconstriction was much more variable and ranged between +29°C and +9°C for different sheep. Foot temperature subsequently fell less rapidly than ear temperature, and at 0°C average foot temperature was 11.0 ± 0.72°C.

At the beginning of the second cold exposure, at +30°C, ear temperatures of the HP8 and LP8 sheep were 1.78°C and 3.26°C higher, respectively, than at the same time on first exposure. Similarly foot temperatures of these groups were 1.70°C and 1.11°C higher at the same time. Significance levels are given in Table 4. There was no significant change in the ear and foot temperatures of the HP30 and LP30 sheep between these occasions. During the second cold exposure, vasoconstriction of the ears and feet of the HP8 and LP8 sheep did not occur until lower ambient temperatures than on first exposure, resulting in higher ear and foot temperatures between +30°C and +12°C (Fig. 3). At 0°C these differences had diminished such that only the foot temperatures of the HP8 sheep were significantly higher on second compared to first exposure. Vasoconstriction, especially in the feet, was slightly delayed in the HP30 and LP30 sheep at the second cold exposure but not sufficiently to produce significant changes in skin temperature.

Table 4. **Significance levels for the differences in mean skin temperature at 1st versus 2nd cold exposure**

Ambient temperatures and times of measurement	Treatment groups	+30°C (10.30 hrs)	+21°C (11.15 hrs)	+12°C (12.00 hrs)	0°C (13.00 hrs)	-15°C 14.00 hrs)
Midside temperature	HP8	NS	NS	NS	NS	NS
	HP30	NS	NS	NS	NS	NS
	LP8	NS	NS	NS	NS	NS
	LP30	NS	NS	NS	NS	NS
Ear temperature	HP8	0.01	0.001	0.02	NS	NS
	HP30	NS	NS	NS	NS	*0.02
	LP8	0.05	0.01	NS	NS	NS
	LP30	NS	NS	NS	NS	NS
Foot temperature	HP8	0.001	0.05	0.01	0.02	NS
	HP30	NS	NS	NS	NS	NS
	LP8	0.02	0.001	NS	NS	NS
	LP30	NS	NS	NS	NS	NS

Differences are either non-significant (NS) or denoted as the probability of the difference being due to chance.

* With this exception, significance levels derive from differences where second exposure values are the higher.

Note the tendency for significant differences to occur mainly amongst the +8 sheep.

Under these experimental conditions vasoconstriction occurred whilst both skin temperature and ambient temperature were falling. The onset of vasoconstriction was therefore defined as the point at which the rate of fall of skin temperature became greater than $0.5^{\circ}C/5$ min. (ambient temperature falling by $1^{\circ}C/5$ min.). This criterion was chosen by reference to the thermal circulation index (Burton and Edholm, 1955), which measures the ratio of external to internal insulation and is given by the formula:-

$$\frac{I_E}{I_T} = \frac{T_S - T_A}{T_R - T_S}$$ in which I_T = tissue insulation, I_E = insulation of the fleece and fleece/air interface, T_R = rectal temperature, T_S = skin temperature and T_A = air temperature. Substitution of typical values for rectal, skin and ambient temperature showed the change in skin temperature which could be expected due to physical cooling effects alone, i.e. with no change in thermal circulation index. If physiological cooling occurred due to vasoconstriction, tissue insulation would increase and therefore the thermal circulation index would decrease. Calculations showed that a fall of skin temperature in the region of $0.30^{\circ}C/^{\circ}C$ fall in ambient temperature could be expected due to physical cooling effects alone, (N.B. midside temperature fell by $0.35^{\circ}C/^{\circ}C$). Three basic assumptions are made in using the index:

(i) that the sheep are in thermal equilibrium,

(ii) that there is no change in sweating rate,

(iii) that the sheep remain perfectly still so that I_E is constant.

These conditions obviously could not be fully satisfied, so the limits for physical cooling were set rather high ($0.5^{\circ}C/^{\circ}C$) to allow for probable errors from these sources. In most cases, however, vasoconstriction was characterized clearly by a sudden change in the rate of fall of skin temperature to

a new rate often exceeding 1°C/°C fall in ambient temperature. This was much more marked than is apparent in Fig. 3, since averaging the data from 10 sheep had a smoothing effect on the curve. Fig. 4 shows individual responses for the ears of the HP8 sheep on first and second exposure. The point of vasoconstriction can be clearly seen for individual sheep.

Table 5 gives the onset of vasoconstriction with respect to ambient and skin temperature. During first cold exposure there was no difference between groups in the ambient temperature at which the ears or feet vasoconstricted. Analysis of variance for second exposure (Table 6) shows that the ears of sheep kept at +8°C between exposures vasoconstricted at lower ambient temperatures compared to those of sheep kept at +30°C, which showed little change. The feet of all groups generally vasoconstricted at lower ambient temperatures on second exposure, especially those of high plane sheep (Table 6). There was no significant effect of exposure to +8°C. Nevertheless, the feet of HP8 and LP8 sheep were appreciably higher during initial stages of second compared to first exposure, whereas those of the HP30 and LP30 sheep were not (Fig. 3). The combination of a slight delay in vasoconstriction coupled with generally reduced rates of fall of foot temperature after vasoconstriction appeared to be responsible for this.

Actual ear and foot temperatures at the onset of vasoconstriction were each very uniform and not influenced by nutritional or temperature treatment. However they were different from each other; vasoconstriction occurred in the ears at higher ambient ($P < 0.001$) and higher skin temperatures ($P < 0.001$) than in the feet.

At ambient temperatures below 0°C spasmodic and rapid increases in ear temperature ranging from 2°C to over 20°C were observed. Fluctuations in foot temperature were rare and never exceeded 4°C. Periodic fluctuations in the

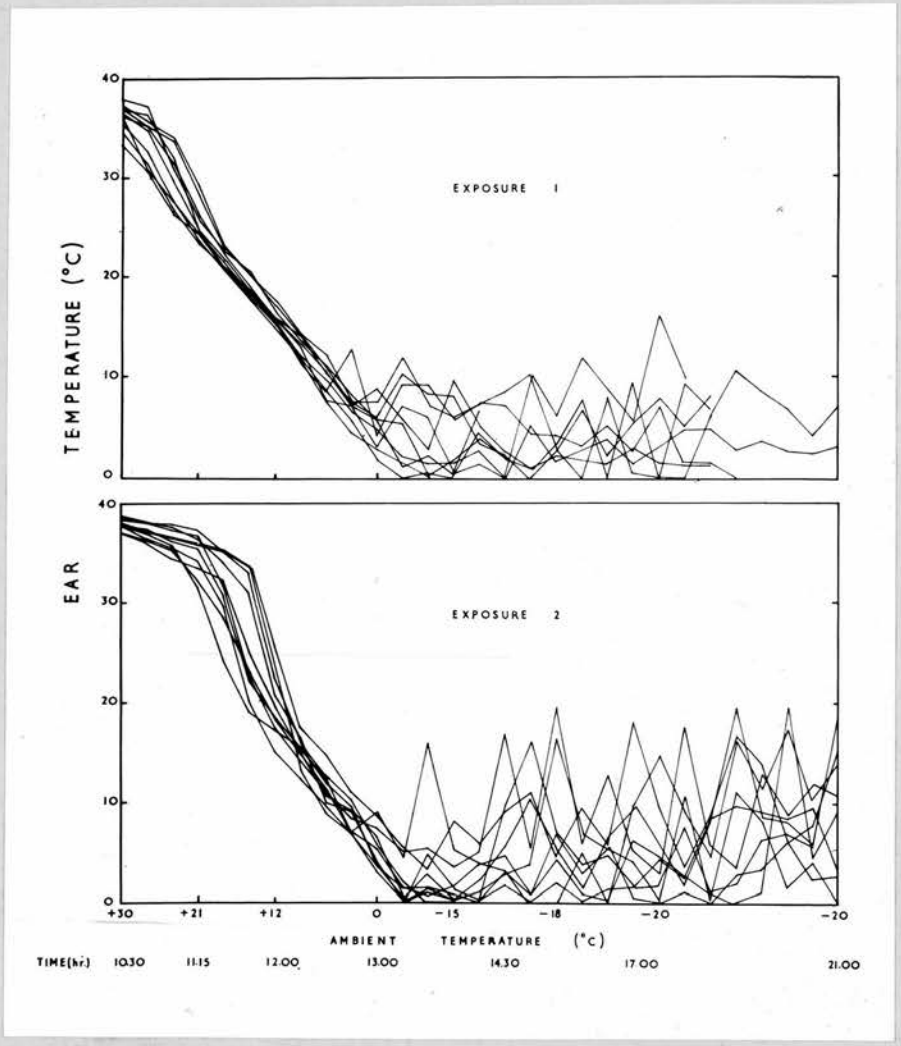


Fig. 4 The changes in ear temperature of 10 individual sheep in the HP8 treatment group during first and second cold exposures.

Values are plotted at 15 min. intervals between 10.30 and 14.30 hrs. and at 30 min. intervals thereafter. Ambient temperature was lowered progressively according to the time scale shown.

Table 5. Mean ambient temperature and ear and foot skin temperature at the onset of vasoconstriction in the ears and feet during 1st and 2nd cold exposures

Treatment group	n	Exposure	Ear Vasoconstriction		Foot Vasoconstriction	
			Ambient temperature °C	*Ear temperature (°C)	Ambient temperature °C	*Foot temperature(°C)
HP8	10	1	26.8 ± 0.70	34.5 ± 0.43	20.0 ± 0.91	31.7 ± 0.56
		2	19.8 ± 1.33	34.9 ± 0.44	10.6 ± 1.51	31.0 ± 0.70
HP30	10	1	25.9 ± 0.81	34.9 ± 0.34	19.7 ± 2.05	31.6 ± 0.80
		2	25.3 ± 1.13	34.1 ± 0.68	13.2 ± 2.38	29.2 ± 0.86
LP8	10	1	27.5 ± 0.53	33.1 ± 0.88	20.3 ± 1.66	30.2 ± 0.13
		2	22.9 ± 1.20	34.7 ± 0.78	15.7 ± 1.55	31.7 ± 0.70
LP30	10	1	27.3 ± 0.60	34.9 ± 0.60	23.2 ± 1.29	32.7 ± 0.74
		2	25.0 ± 1.12	35.2 ± 0.60	19.1 ± 1.73	30.0 ± 1.16

* Ear and foot temperatures were those obtaining immediately prior to vasoconstriction

Table 6. Analysis of Variance - Ambient temperature at onset of vasoconstriction during second acute cold exposure

		Ear			Foot		
Source of Variation	df.	M.S.	F	P	M.S.	F	P
Nutrition	1	19.60	1.37	NS	302.50	9.19	<0.01
Temperature	1	144.40	10.06	<0.01	90.00	2.73	NS
Nutrition x Temperature	1	28.90	2.01	NS	1.60	0.04	NS
Error	36	14.35			32.91		

Table 7. Cold-induced vasodilatations in the ears at sub-zero temperatures

Treatment group	n	Mean total No. of vasodilatations per 100 min. exposure		Mean No. of large vasodilatations per 100 min. exposure	
		1st exposure	2nd exposure	1st exposure	2nd exposure
HP8	10	2.32 ± 0.46	4.73 ± 0.12	0.22 ± 0.08	1.05 ± 0.22
HP30	10	3.45 ± 0.41	2.38 ± 0.44	0.36 ± 0.12	0.52 ± 0.16
LP8	10	3.33 ± 0.47	2.87 ± 0.47	0.17 ± 0.09	0.62 ± 0.31
LP30	10	4.22 ± 0.49	2.81 ± 0.61	0.66 ± 0.25	0.56 ± 0.27

Vasodilatations were defined as temporary fluctuations in skin temperature greater than 1.5°C, or, for large vasodilatations, greater than 10°C.

Table 8. Mean skin temperatures (°C) on the midside, ear and foot between acute cold exposures (days 4 and 14)

Ambient Temperature	+30°C		+8°C	
Day	4	14	4	14
Midside	37.1 ± 0.23	36.8 ± 0.18	29.1 ± 0.46	28.2 ± 0.34
Ear	37.3 ± 0.29	37.0 ± 0.35	12.1 ± 1.01	13.5 ± 1.19
Foot	36.2 ± 0.34	35.4 ± 0.24	17.6 ± 1.89	15.0 ± 1.38

High and low plane nutrition groups were combined.

Each value represents a mean based on 20 sheep.

temperatures of the feet and ears have previously been observed in sheep at sub-zero temperatures by Webster and Blaxter (1966) and mentioned by Slee (1966), and have been termed cold-induced vasodilatation. The duration of each dilation was on average 15-20 min., but individuals showed vasodilatations of varying magnitude and frequency which could not be classified into the two distinct patterns described by Webster and Blaxter (1966). Table 7 shows the general tendency for sheep kept at +8°C to exhibit larger and in the case of the HP8 sheep a greater number of cold vasodilatations ($P < 0.001$), on second exposure. In contrast the frequency and magnitude of cold vasodilatations showed no consistent change in the HP30 and LP30 sheep. The frequency of vasodilatation appeared to be independent of body temperature, since even when body temperature had been depressed by several degrees vasodilatation was frequently observed. Rhythmical cycles of vasodilatation in the ears, termed by Lewis (1930) the 'hunting reaction' and demonstrated in sheep by Webster and Blaxter (1966), were rarely observed in these sheep on first exposure, but did occur more frequently in the HP8 and LP8 sheep on second cold exposure. These findings must however be treated with some reserve in view of the considerable variation between groups at the first cold exposure prior to temperature treatment. The recording equipment was not capable of monitoring temperatures lower than 0°C and extremity temperatures probably fell below this. However Webster and Blaxter (1966) showed that mean shank temperatures of sheep at -10°C fell only 0.7°C below zero. It seems safe to conclude, therefore, that little information was lost, especially as the results were of a comparative nature.

(b) Between acute exposures (days 4 and 14)

Table 8 shows mean midside, ear and foot temperatures of sheep kept at +30°C and +8°C on days 4 and 14. Nutritional groups were combined since no

differences were apparent between groups. No significant changes in midside, ear or foot temperature occurred between days 4 and 14.

3. Heart rate

(a) During acute cold exposures

Heart rates of all groups of sheep showed similar changes during first cold exposure (Fig. 5). As ambient temperature fell from +30°C to +20°C mean heart rate remained at 90 beats/min. Below +20°C rates began to increase linearly and reached 165 beats/min. at 0°C. Below -15°C heartrates remained fairly constant at approximately 220 beats/min. Heart rates of both HP8 and LP8 sheep were significantly faster at +30°C before the second cold exposure than at the same time before first exposure (Table 9). But on second exposure little further change from this elevated value occurred until ambient temperature had fallen much lower than on first exposure (+9°C and +12°C for the HP8 and LP8 sheep respectively). They subsequently increased in the same manner as on first exposure.

Heart rates of the +8 sheep were also significantly elevated at sub-zero temperatures on second exposure compared to first exposure (Table 9). In contrast, heart rates in the +30 sheep were similar during the two exposures. There was no consistent relationship between heart rate and performance or change in heart rate and change in performance between exposures.

(b) Between acute exposures (days 4 and 14)

Heart rates of the HP8 and LP8 sheep (Fig. 6) had increased by 36 ($P < 0.001$) and 44 ($P < 0.001$) beats/min. respectively when measured at +8°C on day 4, by comparison with their values at +30°C before the first exposure. Heart rates of the HP30 and LP30 sheep had also increased by 20 ($P < 0.01$) and 23 ($P < 0.01$) beats/min. respectively during the same period (measured at +30°C on both occasions). Unlike the +8 sheep the heart rates of the +30 sheep had decreased

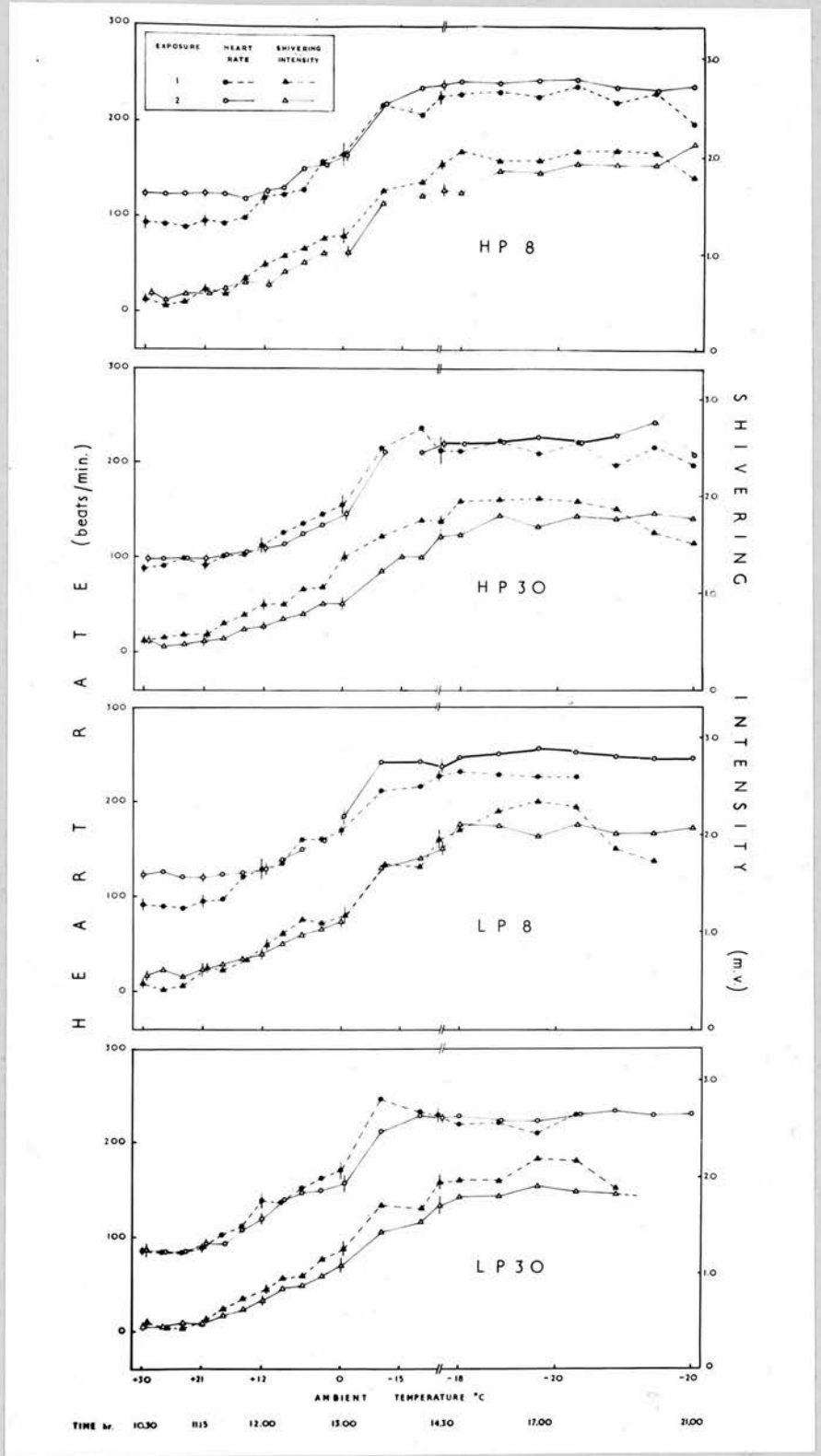


Fig. 5 The changes in mean heart rate and shivering intensity in the four main treatment groups (10 sheep per group) during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown.

Table 9. Significance levels for the differences in mean heart rate during 1st versus 2nd cold exposure

Ambient temperature and times of measurement	n	+30°C (10.30 hrs)	+21°C (11.15 hrs)	+12°C (12.00 hrs)	0°C (13.00 hrs)	-15°C (14.30 hrs)
Treatment group						
HP8	10	0.001	0.01	N.S.	N.S.	0.01
HP30	10	0.05	N.S.	N.S.	N.S.	N.S.
LP8	10	0.001	N.S.	N.S.	N.S.	0.01
LP30	10	N.S.	N.S.	N.S.	N.S.	N.S.

Differences are either non-significant (N.S.) or denoted as the probability of the difference being due to chance.

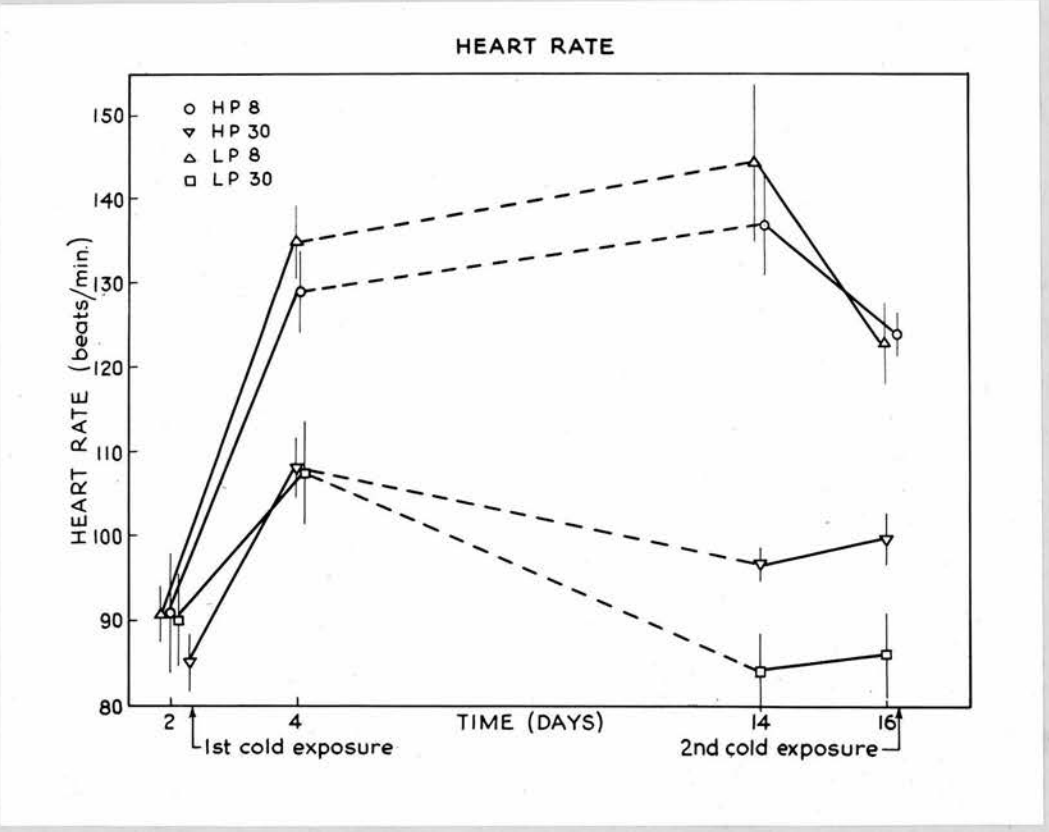


Fig. 6 Mean heart rates in the four main treatment groups (10 sheep per group) before and between acute cold exposures.

On days 2 and 16 the ambient temperature was +30°C for all sheep; on days 4 and 14 the ambient temperatures were +8°C and +30°C according to the temperature treatment between acute exposures.

to their pre-exposure values by day 14. The slight increase in the HP30 and LP30 sheep on day 16 compared to day 14 probably reflects an emotional effect, since this was a single reading taken $1\frac{1}{2}$ hrs. after handling, whereas on day 14 heart rate was the mean measured $1\frac{1}{2}$ to 5 hrs. after handling. Assuming some relationship between heart rate and metabolic rate, both prolonged moderate cold exposure and acute cold exposure would appear to have caused increases in metabolic rate when subsequently measured in a thermoneutral environment.

(c) Emotional effects

The sensitivity of heart rate to emotional factors means that it probably is not a completely reliable index of metabolic rate. Under the present conditions, heart rates were elevated between 09.00 hrs. and 10.00 hrs. on experimental days, presumably due to emotional disturbance. However, mean heart rates of sheep measured at +30°C on days 2 and 14 showed only a non-significant decline from 95 to 85 beats/min. between 10.30 hrs. and 14.30 hrs. Apparently, therefore, there were no important emotional effects after 10.30 hrs. during the periods of measurement. Moreover, the conclusions drawn from this work depend upon comparisons between groups of animals or between experimental occasions where procedures were carefully standardized and extraneous factors would be expected to act equally.

4. Shivering intensity

(a) During acute cold exposure

As ambient temperature fell below 24°C individual sheep began to show signs of shivering, which then increased progressively as ambient temperature fell to zero. Shivering first appeared as tremors in the shoulder muscles. As it increased, the muscles of the rump and flanks became involved, and finally shivering became convulsive and was characterized by large rhythmical

contractions of the major muscles. Fig. 7 shows oscilloscope traces representing different grades of shivering. At sub-zero temperatures convulsive shivering was accompanied by a continual stamping movement of the feet.

Fig. 5 shows the progressive increase in muscle activity of all groups of sheep. During first cold exposure the mean ambient temperature of the onset of shivering was 16.3 $\pm$ 0.50°C. During second exposure, shivering tended to commence at slightly lower ambient temperatures in all groups of sheep. The mean ambient temperature of onset for all groups 14.5 $\pm$ 0.81°C. Although this change was not significant, evidence from visual observations was confirmative. There was no effect of plane of nutrition, or temperature maintained between cold exposures, on the ambient temperature at which shivering commenced. In general, sheep of all groups shivered less on second than on first exposure, and when all measurements of shivering intensity between 14.30 and 16.00 hrs. were pooled, a within animal comparison showed the differences in shivering intensity between first and second cold exposures to be highly significant ($P < 0.001$ in HP8, HP30 and LP30 sheep, $P < 0.02$ in LP8 sheep). The tendency, apparent in Fig. 5, for mean shivering intensity to fall during the later stages of first exposure was associated with the successive removals of the least cold-resistant sheep from the chamber. The most resistant sheep appeared to shiver less than sheep whose body temperature was falling rapidly.

Changes in shivering intensity were closely related to changes in heart rate. When all pairs of readings between +30°C and 0°C from sheep of all groups were combined the correlation coefficients $r = +0.59$ ($P < 0.001$) and $r = +0.67$ ($P < 0.001$) were obtained on first and second cold exposures respectively. However, when correlations were computed using group mean values for heart rate

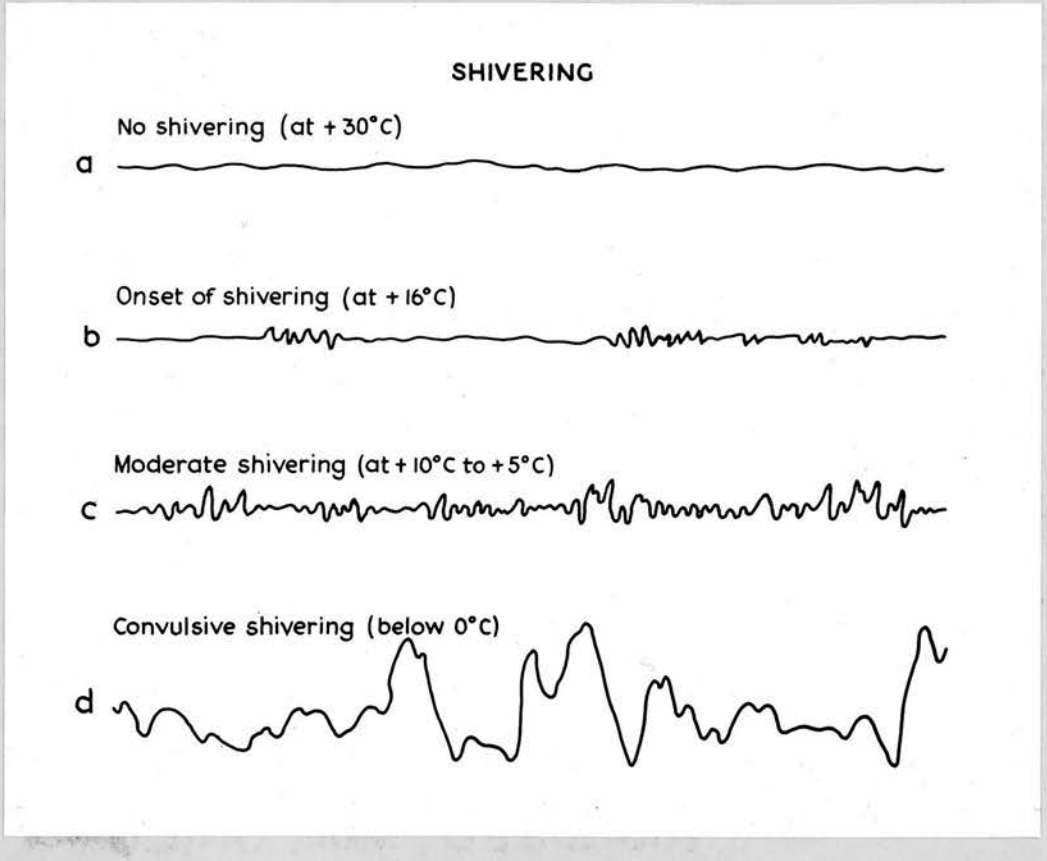


Fig. 7 Typical patterns of shivering during acute cold exposure as displayed by oscilloscope trace.

and shivering, thereby reducing the effects of individual variation, coefficients lying between +0.91 and +0.98 were obtained for all groups on both first and second exposures. This tends to support earlier assumptions regarding the relationship between heart rate and metabolic rate.

(b) Between acute cold exposures (days 4 and 14)

Sheep kept at +8°C between exposures were observed to shiver persistently throughout, though there was a tendency for shivering to become less apparent as exposure progressed. Shivering was never observed in sheep kept at +30°C. E.M.G. recordings were generally confirmative but there was much variation between individuals in patterns of shivering and significant differences could not be demonstrated.

5. Respiration rate

(a) During acute cold exposure

Changes in mean respiration rate during first and second cold exposures are shown in Fig. 8. Rates were very variable, but at 30°C those of high plane sheep were 45/min. higher than those of low plane sheep ($P < 0.001$). These differences and the changes in respiration rate between +30°C and 0°C ambient temperature were comparable to those described by Blaxter et al. (1959). Respiration rates of all groups were minimal at +12°C and at sub-zero temperatures a slight increase in respiration rate occurred, ($P < 0.001$ over all groups). Changes in respiration rate were similar during both exposures.

It was not possible to measure tidal volume accurately. Nevertheless during a series of measurements e.g. throughout an acute cold exposure, major and consistent changes in amplitude of the pneumograph chart recordings were assumed to reflect changes in tidal volume. Between measurement periods one would expect slight variation in amplitude due to the fixing of the belt, but these would be expected to vary in a random manner. Therefore, while it is

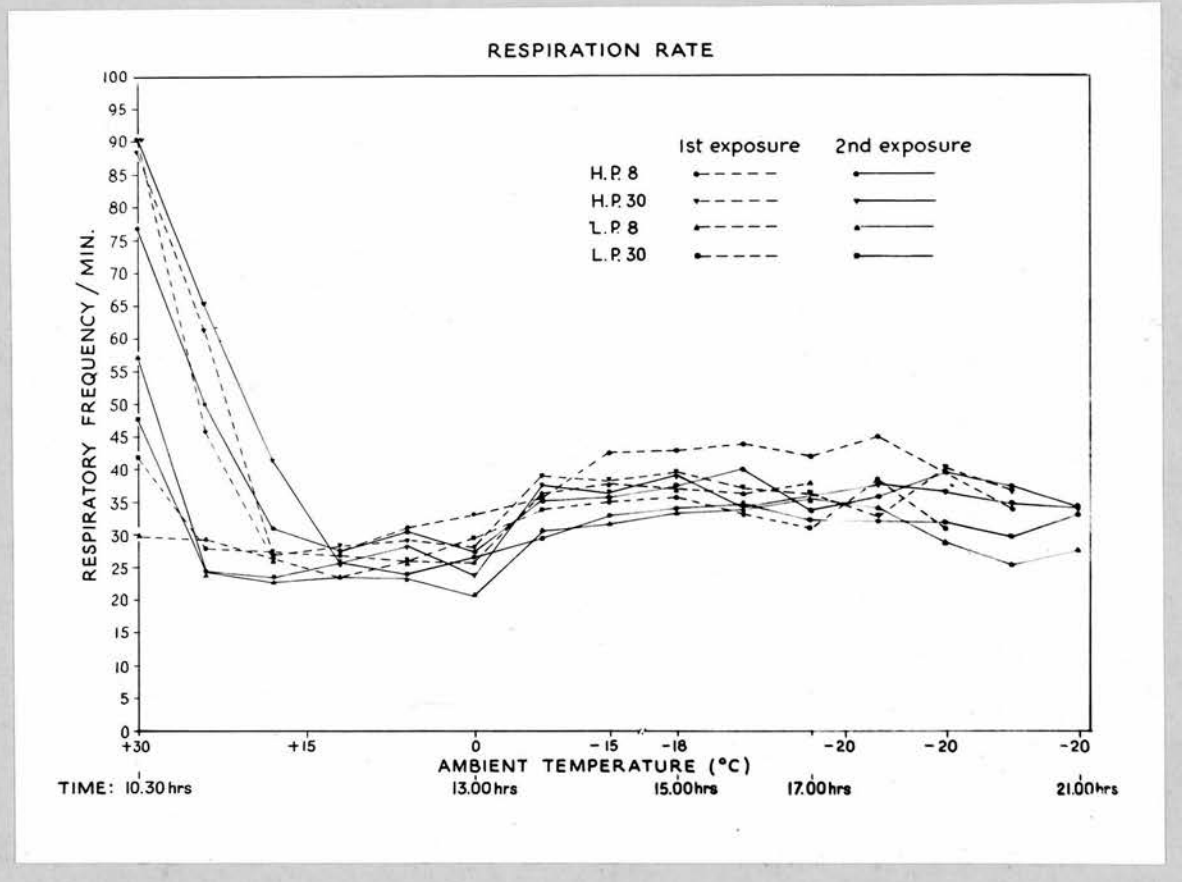


Fig. 8 The changes in mean respiration rate in the four main treatment groups (10 sheep per group) during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown.

Table 10. Mean respiration rates and tidal volumes between acute cold exposures

Treatment groups	n	Respiratory frequency/min.		*Estimated tidal volume (mm)	
		Day 4	Day 14	Day 4	Day 14
HP8	10	45.7 ± 9.2	18.96 ± 0.95	1.72 ± 0.43	2.21 ± 0.45
HP30	10	112.9 ± 7.99	121.80 ± 9.15	0.65 ± 0.11	0.94 ± 0.12
LP8	10	32.0 ± 9.91	22.44 ± 2.72	1.70 ± 0.10	2.28 ± 0.33
LP30	10	70.1 ± 7.95	53.30 ± 9.59	1.31 ± 0.18	1.18 ± 0.21

* Tidal volumes were obtained from averaged kymograph trace amplitudes

recognised that the tidal volume data estimated from pneumograph trace amplitudes are imprecise, they are presented as complementary to the data on respiration rate. During 1st exposure mean 'tidal volume' of all groups, increased by 54% ($P < 0.001$) as ambient temperature fell from +30°C to +12°C, when respiration rates were minimal. Tidal volume further increased by 34% ($P < 0.001$) between ambient temperatures +12°C and -16°C. There was no significant change in 'tidal volume' between first and second exposure.

(b) Between acute cold exposures (days 4 and 14)

Table 10 gives mean respiration rates and 'tidal volumes' on days 4 and 14. High plane sheep generally had higher respiration rates than low plane sheep. Combining values from high and low plane sheep, those kept at +8°C had lower respiration rates ($P < 0.001$) and larger 'tidal volumes' ($P < 0.001$) than sheep kept at +30°C. Throughout the experiment sheep responded to cooler environments by reducing respiration rate while increasing 'tidal volume'.

6. Bodyweight

The low plane ration caused mean bodyweight to remain approximately constant from the time of allocation to treatment until each animal received its first cold exposure, while the high plane ration allowed on average a 30% increase in bodyweight (Table 11). During temperature treatment, between days 1 and 15, 34 out of 40 sheep lost weight, but the HP30 and LP30 sheep showed only 49% of the weight loss of their contemporaries at +8°C. During this period 15 out of 20 high plane sheep refused food, but the amount left was not associated with temperature treatment, weight change, or response to cold exposure. One LP8 sheep refused food and its performance at the second cold exposure was the poorest of the group. There was no consistent relationship between bodyweight and resistance to cooling except in the LP8 sheep at the second cold exposure ($r = +0.79$; $P < 0.01$). At the first exposure bodyweight accounted for only 9%

Table 11

Mean bodyweight (kg.)

Treatment group	n	November 8th 1965*	At 1st cold+ exposure	At 2nd cold+ exposure
HP8	10	26.7 ± 0.83	34.7 ± 1.24	32.3 ± 1.28
HP30	10	27.0 ± 0.69	33.6 ± 1.22	32.3 ± 1.03
LP8	10	26.5 ± 0.99	27.5 ± 1.10	25.5 ± 0.93
LP30	10	26.9 ± 0.68	27.5 ± 1.01	26.6 ± 0.85

* Sheep were in full fleece

+ Sheep were shorn

Table 12. Mean skinfold thickness (mm)

Treatment group	n	Day 1	Day 15
HP8	10	4.1 ± 0.16	4.5 ± 0.40
HP30	10	3.5 ± 0.13	3.5 ± 0.24
LP8	10	3.6 ± 0.16	3.9 ± 0.25
LP30	10	3.3 ± 0.20	3.3 ± 0.17

of the total variation, calculated by regression, in performance of all sheep. However liveweight gain in the three weeks prior to the first cold exposure was associated with good performance over all treatment groups ($r = +0.47$; $P < 0.001$) and accounted for 22% of the variation in performance.

7. Skinfold thickness

Mean skinfold thickness, measured on days 1 and 15 before the first and second acute cold exposures is shown in Table 12. Sheep on high plane nutrition had generally greater skinfold thickness than low plane sheep. Chronic cold exposure caused a small, non-significant, increase in skinfold thickness. Clearly tissue insulation might be related to skinfold thickness, such that low skin temperatures would be associated with greater skin thickness. However there was no relationship between skinfold thickness and midside temperature or resistance to cooling. Although some improvement in performance was shown by sheep kept at +8°C and these sheep showed a general increase in skin thickness, no significant relationship was found between the two.

SUBSIDIARY TREATMENT GROUPS

Changes in rectal temperature during first exposure of the sheep kept at +30°C (habituation controls - HPHC and LPHC) and +8°C (chronic cold exposure sheep - HPCC and LPCC) for two weeks prior to receiving an acute cold exposure, are given in Fig. 9. Substantially the same pattern emerged both in terms of the response to the drop in ambient temperature from +30°C to 0°C and in resistance to sub-zero cold exposure as was shown by the main treatment groups. Whereas HPHC and LPHC sheep maintained a fairly constant body temperature between +30°C and 0°C, body temperatures of the HPCC and LPCC sheep cooled, and at 0°C were 1.10°C ($P < 0.01$) and 0.45°C (N.S.) lower than those of the HPHC and LPHC sheep respectively. Table 13 gives the mean rates of body

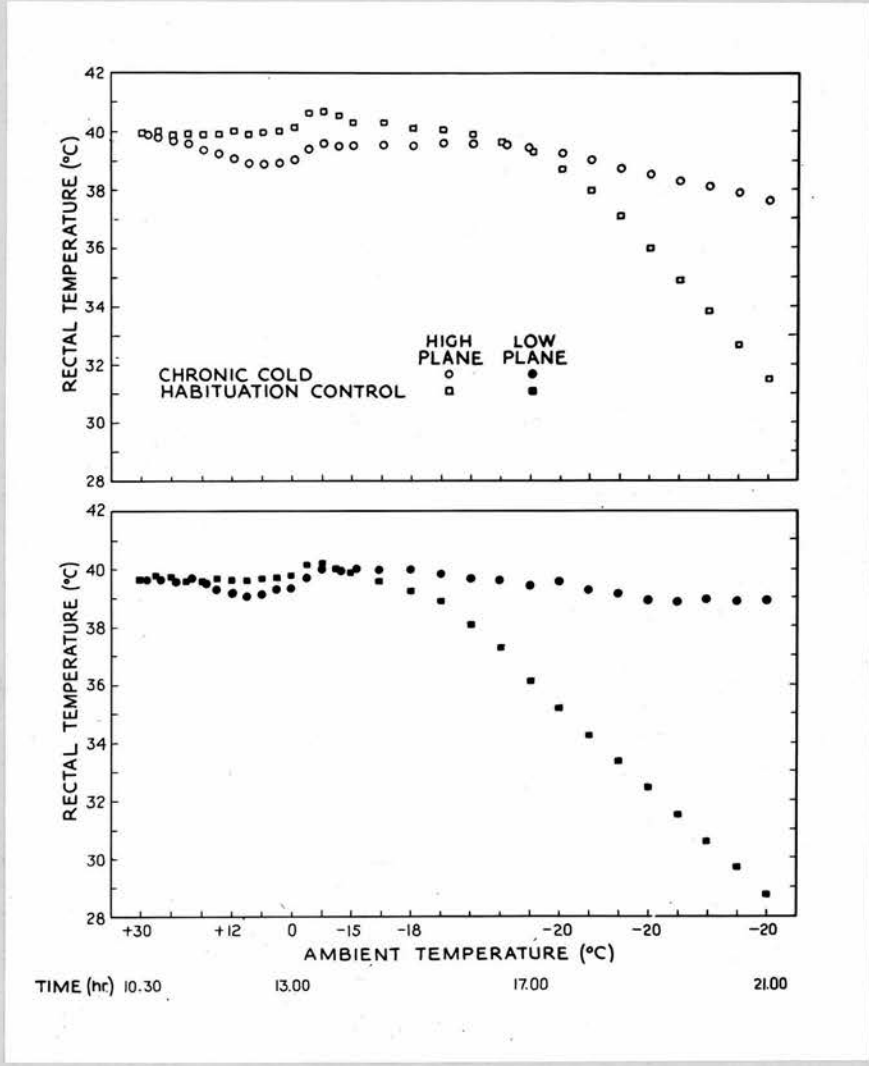
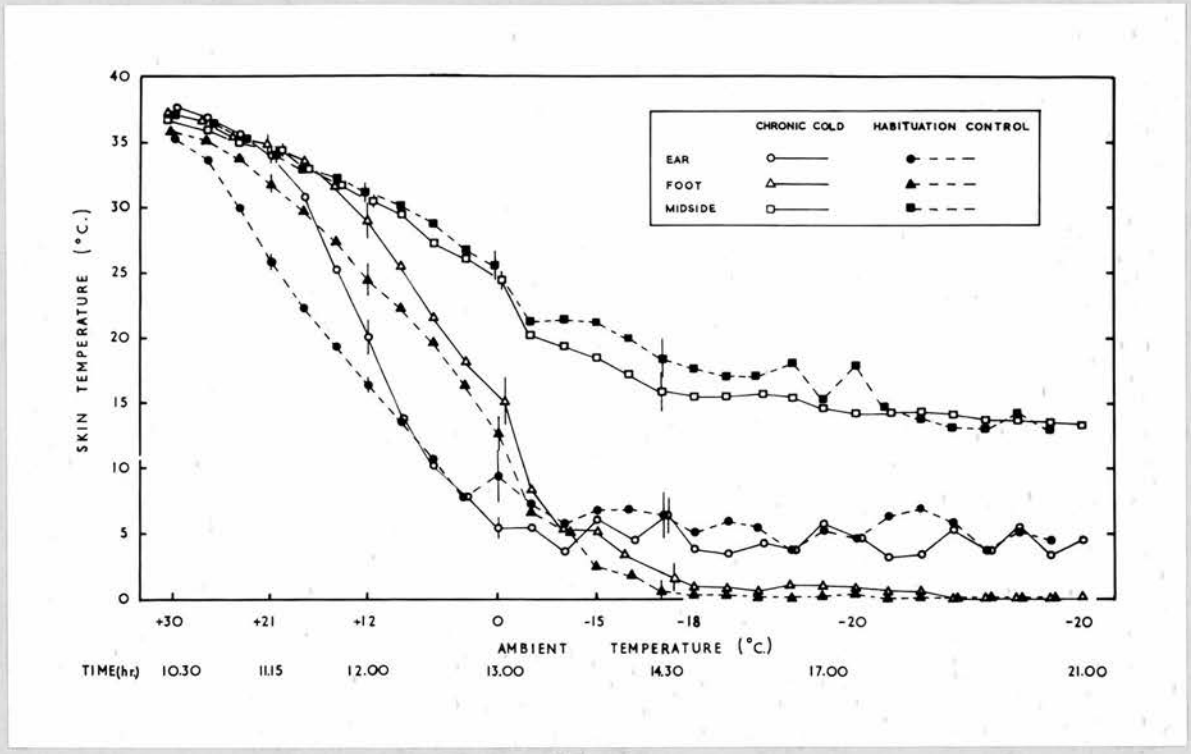


Fig. 9 The changes in mean rectal temperature of high and low plane chronic cold and habituation control groups during first cold exposure.

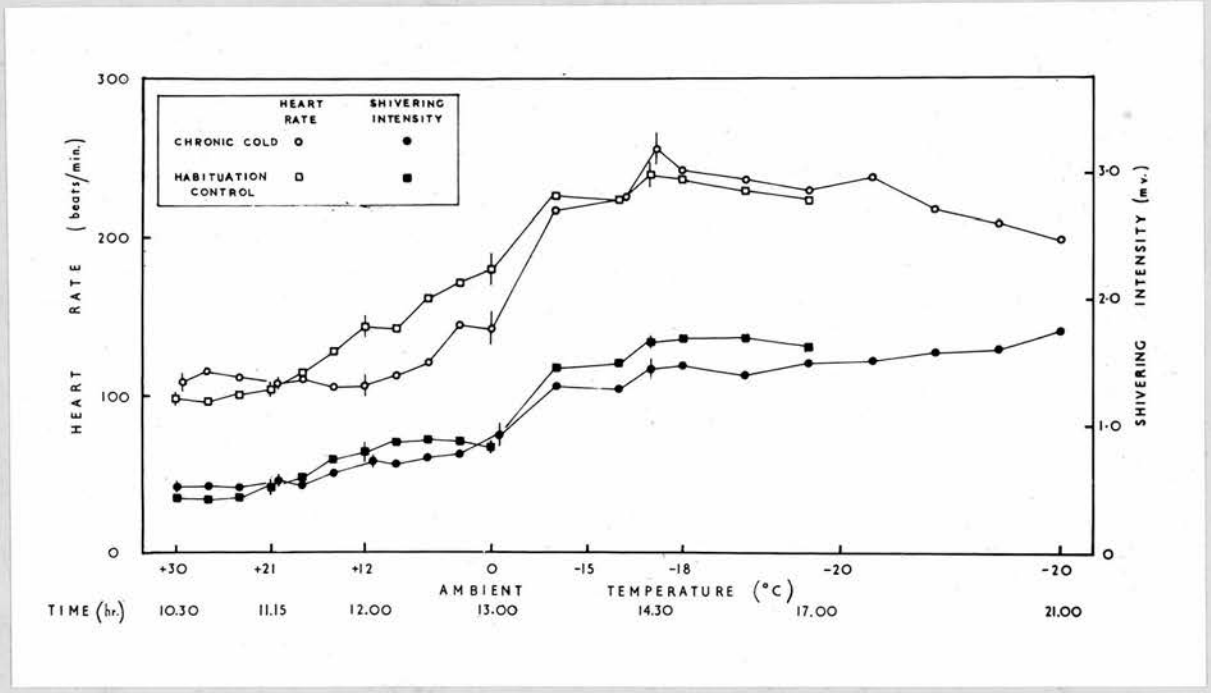
Ambient temperature was lowered progressively according to the time scale shown. Chronic cold groups were kept at +8°C and habituation control groups at +30°C during the two weeks preceding cold exposure.

Table 13. Resistance to Cooling - subsidiary treatment groups

Treatment group	N	Mean rate of decline of rectal temperature (°C/100 mins. cold exposure from 0°C)	P
High plane habituation Control (HPHC)	4	0.888 ± 0.188	<0.01
High plane chronic cold (HPCC)	6	0.273 ± 0.077	
Low plane habituation control (LPHC)	4	1.199 ± 0.088	<0.01
Low plane chronic cold (LPCC)	2	0.093 ± 0.010	



(a)



(b)

Fig. 10 The changes in (a) mean midside, ear and foot temperature and in (b) mean heart rate and shivering intensity in the chronic cold and habituation control groups during first cold exposure.

High and low plane groups were combined and there were 8 sheep per group. Ambient temperature was lowered progressively according to the time scale shown.

cooling. This shows that chronic cold exposure alone was apparently capable of inducing increased resistance to body cooling under acute cold exposure. The similar performance of the HPHC and LPHC sheep after 2 weeks in the climate chamber to that of the main treatment groups at first exposure (Table 3a) confirms that the vast improvement in resistance to cooling of the latter sheep on second cold exposure was an effect of temperature experience rather than of habituation to the climate chamber environment. Habituation, if anything, appeared to have a deleterious effect on performance.

The changes in skin temperature, heart rate and shivering intensity were not significantly affected by nutritional treatment. Nutritional groups were therefore combined and the changes during acute cold exposure are given in Fig. 10. The responses of the HPHC and LPHC sheep were similar to those of all the main groups on first exposure and those of the HP30 and LP30 groups on second exposure. The HPCC and LPCC sheep showed changes in heart rate, shivering and in the onset of vasoconstriction similar to those of the HP8 and LP8 sheep on second cold exposure. Shivering intensity of the HPCC and LPCC sheep was lower between 14.00 and 18.00 hrs. during acute cold exposure than that of the HPHC and LPHC sheep ($P < 0.001$). These results suggest that chronic cold exposure alone was capable of inducing changes similar to those shown by sheep in the main treatment groups experiencing acute and chronic cold exposure.

DISCUSSION

1. Resistance to body cooling

This work has shown that the resistance of Blackface ewe hoggs to body cooling can be increased by previous cold experience involving a) acute exposure sufficient to induce hypothermia and b) chronic exposure to moderately sub-critical temperatures. This effect can be termed acclimatization, and seems similar to that found recently in rodents as a result of short acute cold exposure by Ogilvie (1967a), and Leblanc (1967), and as a result of chronic cold exposure (see review). Work on man has not been strictly comparable, but it is relevant that Budd (1962) and Budd and Warhaft (1966) observed an increase in resistance to body cooling of men during a stay in Antarctica.

The better overall cold resistance of acclimatized compared to non-acclimatized sheep appeared to result from an ability to maintain normal body temperatures for longer and subsequently to sustain slower terminal rates of fall of body temperature. There was no evidence to suggest that this may have been the result of increased insulation. Hart (1963) stated that in rats the total time to death by hypothermia was a two component process depending on the time that metabolic rate could be maintained at elevated levels and the time taken for metabolism to fall to zero. It therefore seems probable that these sheep, after acclimatization, could maintain high metabolic rates for longer and then sustain a less rapid decline in metabolism during cooling. Sheep on high plane nutrition on the other hand, by comparison with low plane sheep, showed relatively fast terminal rates of fall, during both first and second exposure, despite their good overall cold resistance. Nevertheless their terminal rates of fall

were still less on second than on first exposure. Possibly the high plane sheep were able to mobilize greater energy reserves initially during exposure, but used them less economically and subsequently suffered a much more rapid fall in metabolism.

2. Development and retention of acclimatization

Acute sub-zero cold exposure for up to eight hours caused clear acclimatization. Chronic moderate cold exposure (+8°C) for two weeks without acute cold exposure apparently also produced acclimatization on the evidence of the chronic cold and habituation control sheep. But the barely significant additional effect of chronic cold exposure after acute cold exposure (HP8 and LP8 groups of sheep) suggests that these sheep had almost reached their physiological limit for acclimatization after one acute exposure.

The degree of acclimatization shown after acute cold exposure was not related to the length of exposure or the degree of hypothermia induced. Adolph and Richmond (1956) found in hamsters and squirrels that a few hours gradual cooling of both core and skin was more effective than either prolonged exposure to cool air without deep hypothermia or sudden deep hypothermia. After acclimatization their animals had an improved initial resistance to cooling, but did not show the subsequently decreased rate of cooling found in these sheep. Detailed comparisons of the two types of exposure used in this experiment cannot be made on the basis of such small numbers. Nevertheless comparison of the performance of the sheep receiving only acute (HP30 and LP30 sheep) or only chronic cold exposure (HPCC and LPCC sheep) suggested that chronic cold exposure may be as effective as acute cold exposure in inducing acclimatization.

Acclimatization to the acute type of cold exposure was very rapid,

since some exposures lasted for less than four hours, and persisted for at least two weeks. Rapid acclimatization to this type of cold experience has been demonstrated in rodents. Leblanc (1967) has now shown that rats can develop acclimatization after 3 hours cumulative exposure to -20°C, as shown by colonic cooling rates. However, he used 15 separate exposures each of 10 minutes duration over a period of 24 hours. Ogilvie (1967a) found a progressive increase in resistance to body cooling of unrestrained mice during successive 15 minute exposures at -10°C but could not demonstrate the effect in restrained mice. In both cases body temperature during acclimatization was depressed much more than in the sheep.

Sellers, Reichman and Thomas (1951) found that acclimatization was still developing in rats after six weeks chronic cold exposure but was lost within 4 days. Hart (1953c) found that the maximum increase in resistance to death from hypothermia, measured at -17°C, took 4 weeks to develop at +10°C and was almost completely lost after 1 week at +30°C. Fregly (1953) found that 80% of the total decrease in colonic cooling rates of mice at -10°C was developed after six days exposure at +5°C, and Ogilvie (1967b) showed that while much acclimatization was developed after 6-8 days the maximum response occurred only after 14 days at +2°C. The present sheep showed some acclimatization to chronic cold exposure after 14 days, though whether this was a maximal response cannot be ascertained.

Most sheep tested a third time showed a slight but not significant deterioration from their second exposure performance, only two out of the twelve sheep showing any further improvement at the third exposure. Greatest deterioration occurred in those individuals whose resistance had increased most from first to second exposure. These results are difficult to interpret because the second cold exposure not only measured the degree of acclimatization

resulting from the first exposure but could also itself have caused either a further increase in acclimatization or a reduction in existing acclimatization by inducing debility. Nevertheless the results suggest that the limit for acclimatization may have been reached at the second exposure. However, whether the measured response was the maximal one cannot be ascertained, since presumably this merely measured the degree of acclimatization which was retained after 2 weeks at +30°C. It may well be that the response would have been maximal soon after the first exposure.

3. Associated physiological responses

The associated responses were apparently influenced more by chronic sub-critical cold exposure than by acute exposure. At the beginning of the second acute cold exposure the +8 sheep (but not the +30 sheep) showed elevated rectal and skin temperatures and a 40% increase in heart rate when compared to the same time on first exposure. Assuming a good relationship between heart rate and metabolic rate (Blaxter 1948, Webster, 1967) this would mean that basal metabolic rate had increased considerably. Similar work on rodents - Gelineo (1934), Cottle and Carlson (1954), Sellers, Scott and Thomas (1954), Krog, Monson and Irving (1955) and Depocas, Hart and Heroux (1957) has shown basal metabolic rate to be elevated by up to 60% as a result of prolonged cold exposure. It seems probable therefore that an increase in basal metabolic rate had occurred in these sheep. It was probably in consequence that the onset of vasoconstriction, onset of shivering and increase in heart rate of the sheep kept at +8°C occurred at lower ambient temperatures on second than during first exposure.

4. Shivering and non-shivering thermogenesis

The changes in peripheral and core temperatures and in basal metabolism (inferred) were confined largely to the +8 sheep, but improvement in resistance to body cooling was shown by almost all sheep irrespective of whether kept at +8°C or +30°C between acute cold exposures. Similarly sheep of all groups shivered less on second than on first exposure.

As mentioned earlier, much of the work on acclimatization in rodents has demonstrated increased survival times at low temperatures coupled with increased metabolic rates but decreased shivering intensity. Other workers (Davis and Mayer, 1955; Davis, Johnston, Bell and Cremer, 1960) have measured directly the contribution of shivering to total cold-induced thermogenesis in acclimatized and non-acclimatized animals, using curare and diathermy. The general conclusion has been that whereas before acclimatization shivering and non-shivering thermogenesis contribute approximately equally to the total heat production, afterwards the contribution due to shivering is very much reduced. Davis and Johnston (1961) have pointed out that shivering, as it involves a superficial site of thermogenesis, must cause increased blood flow to the skin, and increased convective heat losses due to movement, and a decrease in tissue insulation at the onset of shivering has in fact been reported in sheep by Blaxter et al. (1959). Moreover its efficiency may be reduced by superficial muscle cooling. Non-shivering thermogenesis, on the other hand, being a method of thermogenesis which is compatible with maximal insulation is considered to be more efficient for the maintenance of body temperature.

It seems possible that, in the present sheep, the reduction in shivering intensity after low temperature exposure was associated with some alteration in the site and manner of heat production which enhanced their ability to resist body cooling. Such an explanation is supported by the change in

ratio between heart rate and shivering intensity found during second cold exposure. This presumably indicates an enhanced ability for non-shivering thermogenesis. However in view of the large improvement in resistance to cooling compared to the small reduction in shivering intensity apparently shown in these sheep, it seems likely that other factors also contributed to the production of acclimatization. There was no evidence from the main treatment groups to suggest that shivering intensity was influenced by chronic cold exposure, since both +8 and +30 sheep showed the reduced shivering. But data from the HPCC and LPCC sheep by comparison with that from the HPHC and LPHC sheep did suggest that chronic cold exposure may have some effect.

CONCLUSIONS

Acute cold exposure caused a clear increase in the resistance to body cooling of sheep. Although small numbers were involved, data from the sheep receiving two weeks chronic cold before acute cold exposure suggests that this type of exposure may also be capable of inducing increased resistance to body cooling, increased basal metabolism and other physiological changes in response to cold. In the main treatment groups, however, it is not clear how far these associated responses were actually induced during the period of moderate cold exposure and how far they were caused by the preceding acute exposure and merely allowed to persist during the two weeks exposure to +8°C. The latter is somewhat favoured by the fact that the +30 sheep showed elevated heart rates and rectal temperatures (suggesting elevated basal metabolism) on day 4 but not on day 14. They also showed some delay in foot vasoconstriction during second cold exposure. The assumption then would be that the main acclimatization effect, that is resistance to body cooling, whether caused by acute or chronic cold, could persist through 2 weeks exposure to +8°C or +30°C; but the associated changes, again caused by acute or chronic exposure would tend to decay more quickly unless chronic cold exposure (+8°C) was continued.

PART TWO - SOUTHDOWN AND WELSH MOUNTAIN SHEEP

INTRODUCTION

This experiment was designed to compare two new breeds of sheep, one a down breed, for initial cold resistance and ability to acclimatize to cold. In view of the results from the Blackface sheep it also seemed important to attempt to separate more clearly the effects of chronic moderate cold exposure and acute cold exposure, and to determine whether the effects of chronic exposure were the same whether preceded or followed by acute cold exposure. Southdown and Welsh Mountain sheep were therefore subjected to a modified sequence of temperature treatment, although the actual temperatures used and the standard type of acute cold exposure for measurement of resistance to body cooling were the same as for the Blackfaces. The design also allowed the separation of breed and nutritional interactions in response to the different types of cold exposure.

EXPERIMENTAL PROCEDURE

On October 5th 1966 24 Southdown and 24 Welsh Mountain ewe lambs were equally divided into groups for high and low plane nutrition and subsequent temperature treatment, having been indoors and introduced to the high fibre pelleted ration since September 22nd. The basic high and low plane rations were identical in terms of feed/unit of bodyweight to those used the previous year. All sheep were subjected between December 1966 and June 1967 to a series of double acute cold exposures, but in this experiment each cold exposure was preceeded by 2 weeks at a subcritical (+8°C) or thermoneutral (+30°C) temperature.

On day 1, after close shearing, all sheep entered a climate chamber where the ambient temperature was +30°C. On day 2 at 10.30 hrs. ambient temperature for half the sheep was lowered at a rate of 1°C/5 min. to +8°C and remained there for the next 2 weeks. The remaining sheep were kept at +30°C during this period. On day 16 all sheep were subjected to an acute cold exposure identical to that used in part one (-20°C, 4 m.p.h. wind). For the next 2 weeks the temperature treatments were reversed, those having spent 2 weeks at +8°C were now maintained at +30°C and vice versa. On day 30 all sheep were subjected to a second identical acute cold exposure. The basic experimental plan is presented in Table 14. The experiment therefore consisted of a 2 x 2 x 2 factorial with 6 replicates.

Ambient temperature for sheep kept at +8°C was raised to +30°C 18 hours before each acute cold exposure, i.e. on days 15 and 29 for the respective treatment groups. Sheep kept at +8°C between acute cold exposures (days 17-29) were allowed to recover overnight at +20°C after the first acute cold exposure before the ambient temperature was rapidly lowered to +8°C at 9.30 hrs. next morning.

Table 14. Experimental Plan

Treatment Groups	n	Day 1	Day 2	Day 14	Day 15	Day 16	Day 18	Day 28	Day 29	Day 30
Southdown HP 8-30	6	close	Temp.	CTM	Temp.	1st	CTM	CTM		2nd
Welsh HP 8-30	6	clipped	lowered	"	raised	acute	"	"		acute
Southdown LP 8-30	6	and	to	+8°C → "	to	cold	← " +30°C → "			cold
Welsh LP 8-30	6	entered	+8°C	"	+30°C	exposure	"	"		exposure
Southdown HP 30-8	6	chamber	CTM	"		"	"	"	Temp.	"
Welsh HP 30-8	6	at	"	"		"	"	"	raised	"
Southdown LP30-8	6	+30°C	← "	+30°C → "		"	← " +8°C → "		to	"
Welsh LP 30-8	6		"	"		"	"	"	+30°C	"
				re-shorn	re-shorn			re-shorn	re-shorn	

CTM = Days when measurements were made at constant temperature

HP = High Plane nutrition

LP = Low " "

8-30 = Temperature sequence - 2 weeks at +8°C - then 1st acute cold exposure - 2 weeks at +30°C - then 2nd acute cold exposure

30-8 = " " - 2 weeks at +30°C - " " " " " - 2 weeks at +8°C - " "

During cold exposure, rectal temperature, skin temperature, heart rate, shivering intensity and respiratory rate were measured as in 1965-66. Similarly, measurements were made at the beginning and end of the constant temperature periods, i.e. on days 2, 14, 18 and 28. In the case of sheep experiencing the temperature sequence 8-30, measurements on day 2, when ambient temperature was lowered to +8°C, were made every 15 minutes as during acute cold exposure. This continued until 12.30 hrs. (ambient temperature +8°C) when the normal half-hourly recordings were made.

The previous technique for measurement of heart rates and shivering intensity was slightly modified. Tin plate electrodes 1½" square were used on the same sites as the needle electrodes in 1965-66. These were strapped to the sheep over a finely shaved site smeared with either electrode jelly, or industrial soft soap. It was thought that sampling a larger area would give a more representative measure of muscle activity.

The feeding regime was like that adopted in 1965-66, viz. all sheep received maintenance rations on days 1, 15 and 29, and no food on days 16 and 30 until after cold exposure. Half maintenance rations were fed before measurements on days 2, 14, 18 and 28 and made up to full rations afterwards. On all other days the normal high- and low-plane rations were fed.

All sheep were reshorn on days 12, 15, 26 and 29. Bodyweight was recorded after shearing on days 1, 15 and 29, and at the same times measurements of skinfold thickness were made.

RESULTS

Throughout the results and discussion sheep on high and low plane nutrition are referred to as HP and LP sheep, while the two sequences of temperature treatment are referred to as 8-30 and 30-8. Thus for example, Southdown sheep on high plane nutrition and exposed to +8°C and then +30°C are referred to as Southdown HP8-30, while similar sheep exposed to +30°C and then +8°C are referred to as Southdown HP30-8. The other six treatment groups are abbreviated accordingly.

The responses of sheep just prior to and during acute cold exposures (days 16 and 30) are again considered separately from those occurring before and between acute cold exposures (days 2, 14, 18 and 28) when sheep were exposed to +8°C or +30°C.

1. Rectal temperature

(a) During acute cold exposure (days 16 and 30)

Fig. 11 shows the changes in mean rectal temperature during first and second cold exposures. There was no difference in rectal temperature between groups with respect to breed and plane of nutrition when measured at +30°C before cold exposure. Sheep which had been kept at +8°C whether in the sequence 8-30 or 30-8 had slightly higher rectal temperatures than their contemporaries which had been kept at +30°C. Between groups the differences did not achieve statistical significance, but within individuals over all groups the mean difference was 0.12°C ($P < 0.01$).

Rectal temperatures of sheep kept at +30°C during the 2 weeks preceding acute exposure whether in the sequence 8-30 or 30-8, invariably cooled slightly as ambient temperature fell to 24°C during acute exposure,

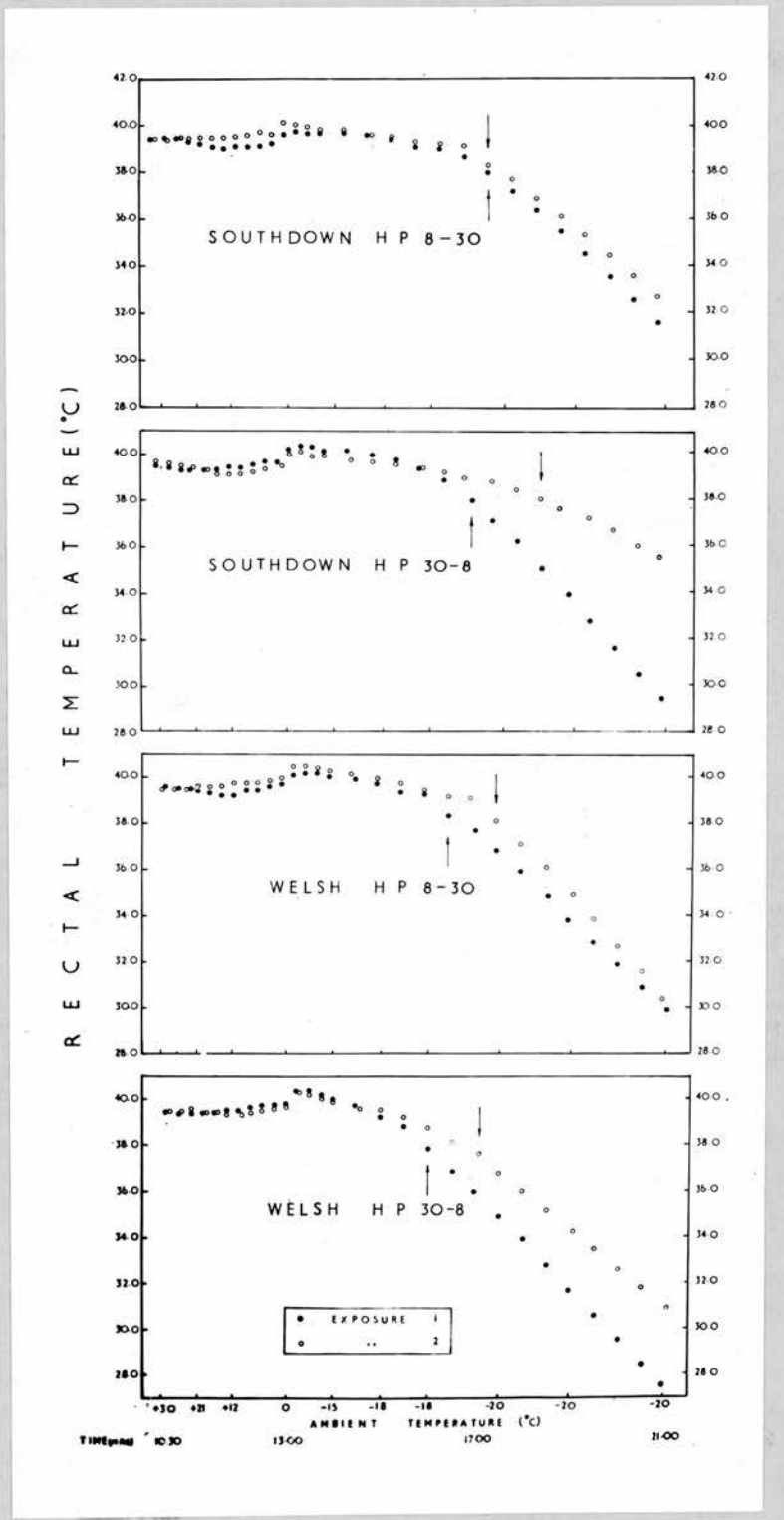


Fig. 11a. The changes in mean rectal temperature in the high plane Southdown and Welsh 8-30 and 30-8 treatment groups (6 sheep per group) during first and second cold exposures.
Ambient temperature was lowered progressively according to the time scale shown. Arrows indicate the point on each line where extrapolation became necessary for more than two individuals per group.

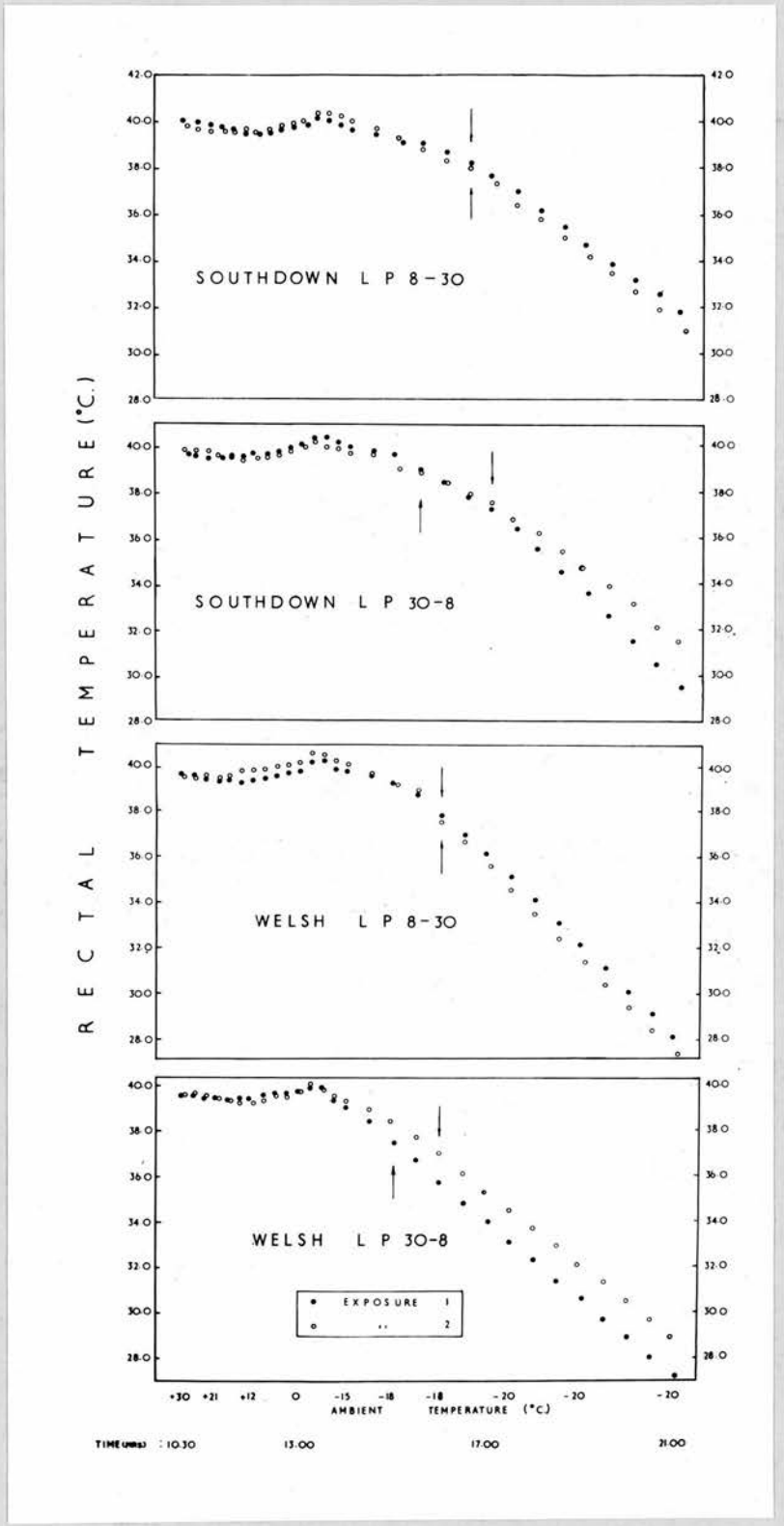


Fig. 11b. The changes in mean rectal temperature in the low plane Southdown and Welsh 8-30 and 30-8 treatment groups (6 sheep per group) during first and second cold exposures. Ambient temperature was lowered progressively according to the time scale shown. Arrows indicate the point on each line where extrapolation became necessary for more than two individuals per group.

and then gradually increased between 24°C and 0°C. Sheep kept at +8°C before acute exposure however, allowed a much greater and persistent fall in rectal temperature during this period, Fig. 11. Only when ambient temperature had fallen much lower did rectal temperature begin to increase. Over all groups mean rectal temperature of sheep previously kept at +8°C fell by 0.38°C ($P < 0.001$) between +30°C and +12°C during acute cold exposure, whereas rectal temperatures of sheep previously kept at +30°C did not change significantly.

The characteristic rise in rectal temperature on sudden rapid cooling from 0°C was observed in all groups of sheep. Although there was no consistent relationship within groups between the extent of this rise and the subsequent resistance to cooling, over all groups there was a positive relationship ($r = +0.38$, $P < 0.001$). This derives partly from the fact that high plane sheep showed, in general, a greater rise than low plane sheep, while showing greater resistance to cooling. A similar response on initial exposure of sheep to cold has been observed by Joyce and Blaxter (1964a), Slee (1966) and Webster (1966), and it is probably due to an overshoot in metabolism coupled with insulative vasomotor changes. It can possibly be explained by the concepts of Hardy (1961), amplified by Webster (1966), such that on cold exposure the increase in heat production is controlled by stimuli proportional to the rate of change of temperature of peripheral receptors, as well as those proportional to the absolute temperature change of peripheral and central receptors. In shorn sheep subject to rapid cooling a large stimulus from peripheral receptors probably causes the overshoot in metabolism.

As with the Blackface data, rectal temperatures of sheep removed from the climate chamber when rectal temperature had fallen to 37.5°C were extrapolated to the maximum exposure time on the basis of individual rates

of fall in the final 30 min. of exposure. Fig. 11 shows the general tendency for slower rates of body cooling after 2 weeks exposure to +8°C whether comparisons are made between groups at first cold exposure, or within the 30-8 temperature treatment groups between first and second cold exposures. Also apparent is the fact that sheep in the 8-30 temperature treatment groups showed little change in performance between first and second cold exposures.

Table 15 gives the mean rates of body cooling of the 8 treatment groups during first and second cold exposures. Analysis of variance, Table 16, shows that on first exposure, breed, plane of nutrition and previous temperature treatment had similar and significant influence on the total variation in resistance to body cooling. On average, Southdown sheep cooled at a rate 32% slower than Welsh sheep, high plane sheep cooled 34% slower than low plane sheep, while sheep kept at +8°C before exposure cooled 33% slower than their contemporaries kept at +30°C. On second acute cold exposure the performance of the two temperature treatment groups 8-30 and 30-8 within each breed x nutrition group were similar; sheep kept at +8°C between first and second cold exposure showed a slight improvement in performance, while sheep kept at +30°C showed little change or even a slight deterioration. The sequence of temperature treatment, therefore, did not appear to influence the final performance of the sheep after similar cumulative cold experience. Only prolonged exposure to +8°C appeared to influence subsequent resistance to body cooling. No additional effect of acute cold exposure could be demonstrated. This would have been apparent as an improved performance of the 8-30 groups of sheep on second cold exposure. Although there were differences between groups with respect to breed and plane of nutrition in initial resistance to body cooling, analysis of

Table 15. Resistance to cooling

Treatment group	n	Rate of decline of rectal temperature (°C/100 min. exposure below 0°C)		Rate of decline of rectal temperature at 2nd exposure compared with 1st exposure (%)
		1st exposure	2nd exposure	
Southdown HP 8-30	6	0.616 ± 0.041	0.785 ± 0.091	127.4
" " 30-8	6	0.922 ± 0.085	0.612 ± 0.114	66.4
Welsh HP 8-30	6	0.966 ± 0.123	0.928 ± 0.058	96.1
" " 30-8	6	1.345 ± 0.122	0.929 ± 0.054	69.1
Southdown LP 8-30	6	1.110 ± 0.221	1.200 ± 0.206	108.1
" " 30-8	6	1.289 ± 0.278	1.172 ± 0.366	90.9
Welsh LP 8-30	6	1.202 ± 0.153	1.448 ± 0.146	120.5
" " 30-8	6	2.236 ± 0.459	1.483 ± 0.157	66.3

Table 16. Analyses of variance - rate of decline of rectal temperature (°C/100 min. exposure)

Source of Variation	df.	1st exposure			Ratio between 1st and 2nd exposure		
		M.S.	F	P	M.S.	F	P
Breed	1	2.462	8.23	<0.01	0.040	0.53	NS
Nutrition	1	2.964	9.91	<0.01	0.075	1.01	NS
*Temperature	1	2.703	9.04	<0.01	2.191	29.57	<0.001
Breed x Temperature	1	0.647	2.16	NS	0.010	0.13	NS
Breed x Nutrition	1	0.053	0.18	NS	0.023	0.31	NS
Nutrition x Temperature	1	0.210	0.70	NS	0.005	0.07	NS
B x N x T	1	0.458	1.53	NS	0.239	3.23	NS
Error	40	0.299			0.074		

* Before or between acute cold exposures

variance (Table 16) showed that the degree of improvement between first and second cold exposure was mainly and highly significantly influenced by the chronic cold temperature treatment. An interesting feature of the data was the comparatively small effect of chronic cold exposure on subsequent resistance to cooling in the Southdown low plane sheep. This was consistently shown during both acute cold exposures.

The improvement in resistance to cooling shown by sheep kept at +8°C appeared to result simply from an enhanced ability to maintain body temperature near normal since, once the decline began, rectal temperatures of sheep kept at +30°C or +8°C before first or second acute cold exposures fell at similar rates. This was in contrast to the Blackface results.

Both breed and plane of nutrition accounted for a significant proportion of the initial resistance to body cooling, but they were also associated with differences in bodyweight. Southdown sheep were considerably heavier than Welsh sheep (Table 27). There were considerable, though non-significant, differences between within-group regression coefficients relating bodyweight and resistance to cooling, and the common regression coefficient was non-significant ($b = +0.024 \pm 0.089$). The possibility that the superiority of the Southdown sheep may have been due solely to their greater bodyweight cannot therefore be conclusively rejected, but correction by means of this regression coefficient suggested that it was not.

(b) Before and between acute cold exposures (days 2, 14, 18 and 28)

Figure 12 shows mean rectal temperatures of sheep on six occasions; after the sheep had remained undisturbed for 1½ hrs. at +30°C before the first and second cold exposures (i.e. days 16 and 30) and between 10.30 hrs. and 14.30 hrs. on days 2, 14, 18 and 28 at the treatment temperatures of

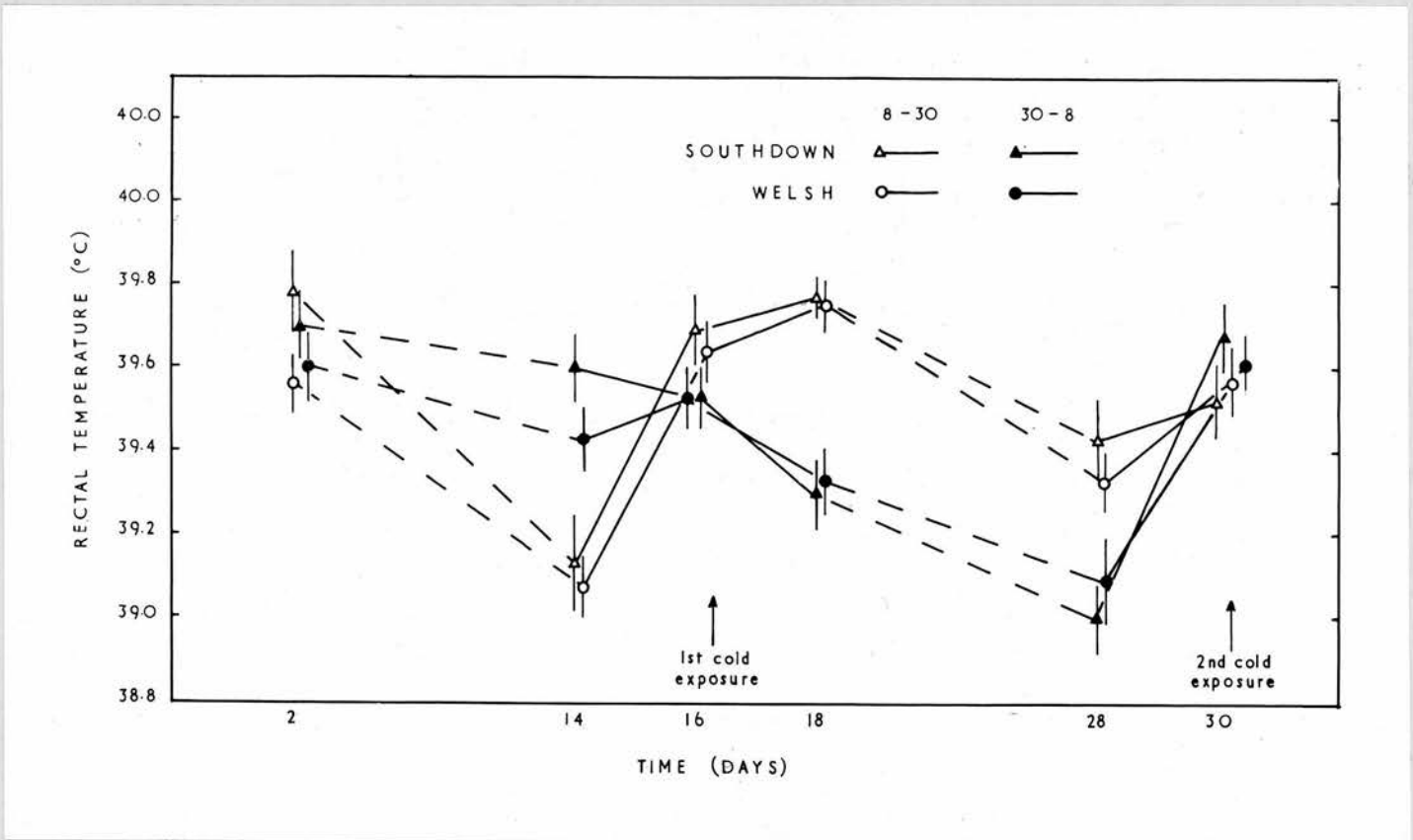


Fig. 12. Mean rectal temperatures in the breed and temperature treatment groups (12 sheep per group) before and between acute cold exposure.

High and low plane groups were combined. On days 16 and 30 the ambient temperature was +30°C for all sheep; on days 2 and 14 the ambient temperatures were +8°C and +30°C according to the temperature treatment imposed on the group, while on days 18 and 28 these temperatures were reversed.

+30°C and +8°C. High and low plane nutrition groups were combined since there were no significant differences between them.

There were no consistent differences in rectal temperature between the two breeds of sheep, and therefore breed groups were combined. Rectal temperatures of sheep at +8°C and +30°C were similer on day 2. The 8-30 sheep had then been at +8°C for 2 hours after the controlled lowering of ambient temperature from +30°C. By day 14 however, rectal temperatures of sheep at +8°C (8-30 sheep) had fallen while those sheep at +30°C showed no change. The difference between groups at this time was 0.42°C ($P < 0.001$). On day 18, when temperature treatments had been reversed (after cold exposure on day 16), rectal temperature of the sheep now at +8°C were 0.44°C ($P < 0.001$) lower than those of sheep at +30°C. By day 28 rectal temperatures of both groups had fallen slightly, but those of sheep at +8°C were still 0.33°C ($P < 0.001$) lower than those of sheep at +30°C. It seems probable that rectal temperatures of the 8-30 sheep on day 18 were elevated as a result of the acute cold exposure experienced 2 days previously. The effect of two weeks exposure to +8°C on rectal temperature measured at +30°C (10.30 hrs.) before cold exposure on days 16 and 30, is also clearly shown in Fig. 12. Within individual sheep rectal temperatures were 0.12°C ($P < 0.01$) higher after 2 weeks at +8°C than after a similar period at +30°C. An interesting feature of Fig. 12 is that it shows the easily reversible nature of the temperature treatment effects on rectal temperature. These findings are in accord with the Blackface data, and add support to the conclusions regarding the effects of cold exposure on metabolic rate.

(c) Emotional effects

Sheep kept at +30°C on constant temperature measurement days (2, 14, 18

and 28) showed a significant ($P < 0.01$) fall in body temperature of 0.2°C between 10.30 hrs. and 12.30 hrs. This was similar in magnitude to that observed in the Blackface sheep. It suggests that the slight cooling shown by 30-8 sheep on first exposure and by 8-30 sheep on second exposure as ambient temperature fell from +30 to +24°C may have been the result of a decay of emotional effects due to handling coupled with possible diurnal changes.

(d) Variation in performance

Considerable variation in cold resistance was observed between individuals. The within breed coefficients of variation, Table 17, suggest that this was similar in the Southdown and Welsh breeds, but that there was generally more variation between individuals on low than on high plane nutrition. The Blackface sheep on the other hand, page 25, tended to show less variation among low plane than among high plane sheep. There was no apparent reason for the difference other than the small numbers used for the estimates of variation. Also shown in Table 17 is the greater variation in performance between sheep kept at +30°C prior to acute cold exposure compared to those kept at +8°C

Individual repeatability of performance between first and second exposures was high, ranging from 0.50 to 0.96 for the eight treatment groups. Pooling breed and nutrition groups, repeatability of performance within the 30-8 and 8-30 temperature treatment groups was 0.77 and 0.78 respectively ($P < 0.001$ in both cases). By comparison with the Blackface data, page 25, one would have expected a lower repeatability estimate after the 30-8 treatment as a result of acclimatization induced between first and second cold exposure. This was not the case, which suggests that the 30-8 sheep

Table 17. Variation in Resistance to Cooling

	Mean rate of decline of rectal temperature (°C/100 min.)	σ^2*	Coefficient of Variation (%)
Southdown	0.984	0.203	46
Welsh	1.437	0.395	44
High	0.962	0.058	25
Low	1.459	0.540	50
1st exposure after 2 weeks at +30°C	1.448	0.465	47
1st exposure after 2 weeks at +8°C	0.973	0.133	37

In the calculation of variation within breeds, values for nutritional and temperature treatment groups on first exposure were combined.
In the calculation of variation within nutritional groups, values for breed and temperature treatment groups on first exposure were combined.
In the calculation of variation within temperature treatments, breed and nutritional groups at first exposure were combined.
*Within group variance (residual) after removal, by analysis of variance, of the variation between groups resulting from the treatment imposed.

showed a relatively uniform degree of acclimatization or that the change was small in comparison with the variation in performance between individuals and did not affect the rankings. The latter seems most probable.

2. Skin temperature

(a) During acute cold exposure (days 16 and 30)

Fig. 13 shows the changes in mean midside, ear and foot temperatures during first and second acute cold exposures. When measured at +30°C before cold exposure, midside temperatures of all groups of sheep except the Welsh LP30-8 were slightly higher following 2 weeks exposure to +8°C than after 2 weeks at +30°C., whether in the 8-30 or 30-8 temperature sequence (Table 18). Over all groups the difference was 0.43°C ($P < 0.001$). During cold exposure, midside temperatures fell gradually at an overall mean rate of 0.34°C/°C fall in ambient temperature, a rate similar to that shown by the Blackface sheep in the first experiment. In the case of the Southdown LP30-8, Welsh HP8-30, Welsh HP30-8 and the Southdown HP8-30 sheep midside temperatures remained slightly, though in general not significantly, higher throughout cold exposure when this followed 2 weeks exposure to +8°C Fig. 13 and Table 18. This was especially so for the Welsh HP8-30 group. Little change was observed in other groups. It seems possible that this may have been a chance effect resulting from the small numbers involved especially since no such difference had been observed in the Blackface sheep. There were no significant differences in midside temperature between groups due to breed or plane of nutrition. No significant relationship was found between midside temperature and resistance to cooling.

Ear and foot temperatures of sheep kept at +8°C for 2 weeks were higher

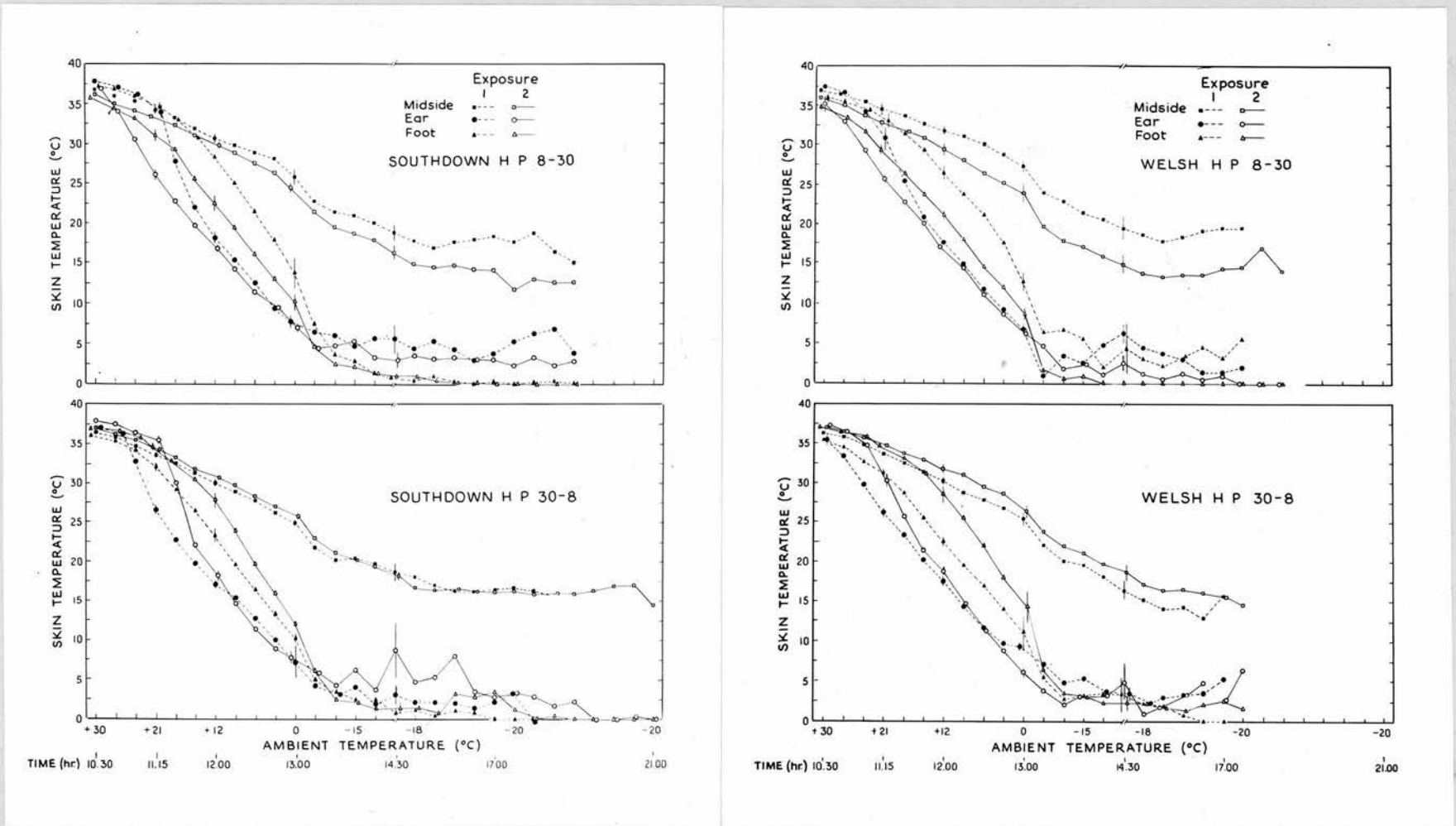


Fig. 13a. The changes in mean midside, ear and foot temperature in the high plane Southdown and Welsh 8-30 and 30-8 temperature treatment groups (6 sheep per group) during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown. Standard errors are denoted by vertical lines. At +30°C they were generally too small to show on this scale.

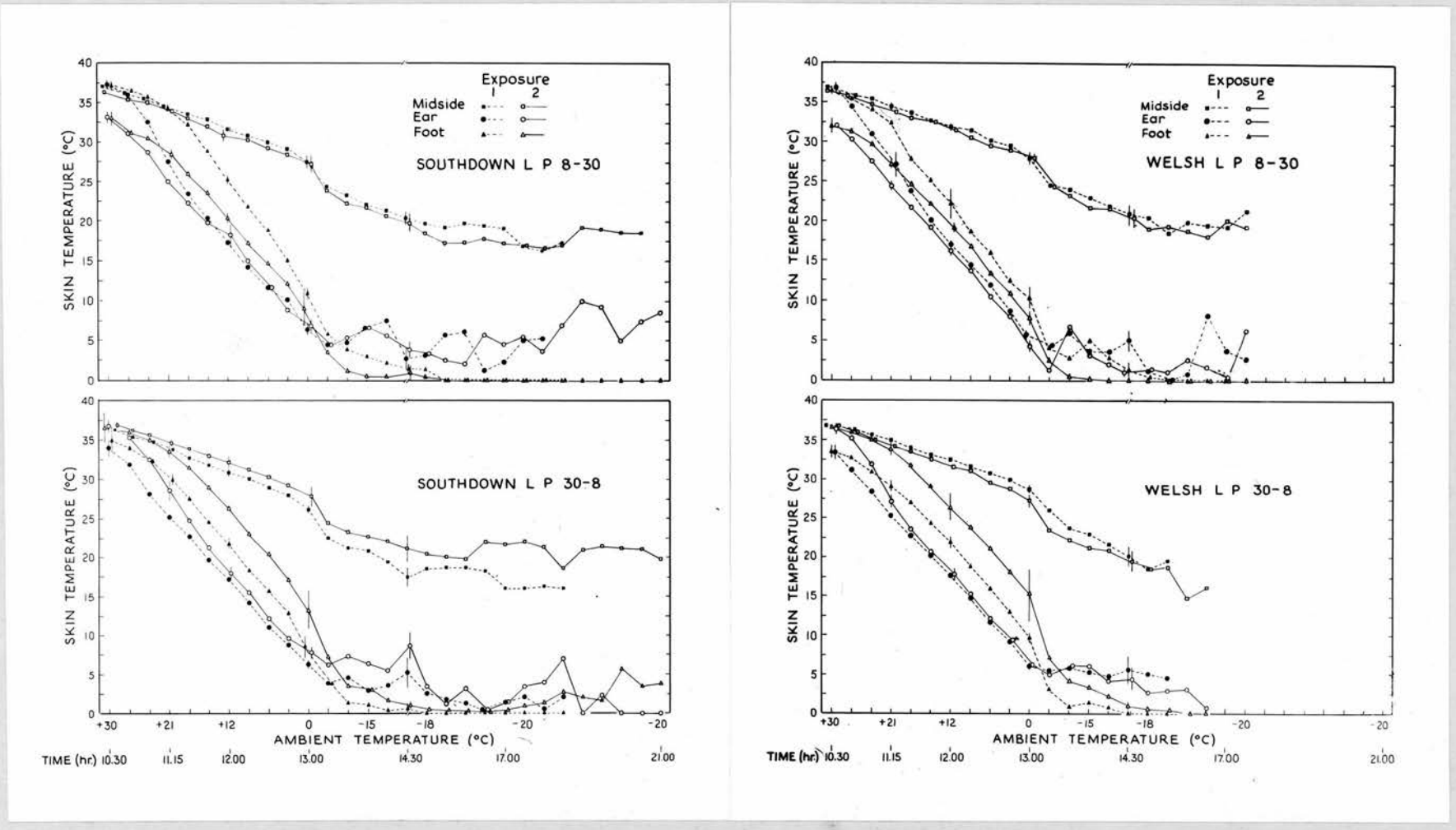


Fig. 13b. The changes in mean midside, ear and foot temperature in the low plane Southdown and Welsh 8-30 and 30-8 temperature treatment groups (6 sheep per group) during first and second cold exposures.

Ambient temperature was lowered progressively according to the time scale shown. Standard errors are denoted by vertical lines. At +30°C they were generally too small to show on this scale.

Table 18. Mean skin temperature before 1st and 2nd acute cold exposure, and significance levels of the differences in mean skin temperature at 2nd compared to 1st exposure

Parameter and treatment group			n	Skin temperature		Direction of the difference at 2nd compared to 1st exposure and significance levels				
						Ambient temperature and time of measurement				
				+30° before 1st exposure	+30° before 2nd exposure	+30° (10.30hrs)	+21°C (11.15hrs)	+12°C (12.00hrs)	0°C (13.00Hrs)	-15°C (14.30hrs)
	Southdown	HP8-30	6	36.8 ± 0.22	36.2 ± 0.33	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)
	"	HP30-8	6	36.4 ± 0.15	36.9 ± 0.18	+ (N.S.)	+ (N.S.)	+ (N.S.)	+ (N.S.)	- (N.S.)
	Welsh	HP8-30	6	37.1 ± 0.14	36.1 ± 0.27	- (N.S.)	- (0.02)	- (0.05)	- (N.S.)	- (N.S.)
MIDSIDE	"	HP30-8	6	36.2 ± 0.28	36.9 ± 0.24	+ (N.S.)	+ (N.S.)	+ (0.02)	+ (N.S.)	+ (N.S.)
TEMPERATURE	Southdown	LP8-30	6	36.9 ± 0.17	36.4 ± 0.22	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)
	"	LP30-8	6	36.5 ± 0.07	36.9 ± 0.25	+ (N.S.)	+ (0.05)	+ (N.S.)	+ (N.S.)	+ (0.05)
	Welsh	LP8-30	6	37.0 ± 0.11	36.5 ± 0.11	- (N.S.)	- (N.S.)	- (N.S.)	+ (N.S.)	- (N.S.)
	"	LP30-8	6	37.0 ± 0.18	36.8 ± 0.31	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)
	Southdown	HP8-30	6	37.9 ± 0.29	37.0 ± 0.47	- (N.S.)	- (0.001)	- (N.S.)	- (N.S.)	- (N.S.)
	"	HP30-8	6	37.1 ± 0.35	38.1 ± 0.23	+ (0.001)	+ (0.001)	+ (N.S.)	+ (N.S.)	+ (N.S.)
	Welsh	HP8-30	6	37.6 ± 0.24	35.1 ± 0.94	- (0.05)	- (0.02)	- (N.S.)	- (N.S.)	- (N.S.)
EAR	"	HP30-8	6	35.4 ± 0.89	37.3 ± 0.09	+ (N.S.)	+ (0.01)	- (N.S.)	- (N.S.)	+ (N.S.)
TEMPERATURE	Southdown	LP8-30	6	37.3 ± 0.40	33.2 ± 0.72	- (0.01)	- (0.05)	+ (N.S.)	+ (N.S.)	+ (N.S.)
	"	LP30-8	6	33.9 ± 0.95	36.8 ± 0.69	+ (0.05)	+ (0.05)	+ (N.S.)	+ (N.S.)	+ (N.S.)
	Welsh	LP8-30	6	36.9 ± 0.45	32.2 ± 0.24	- (0.001)	- (N.S.)	- (N.S.)	- (N.S.)	- (N.S.)
	"	LP30-8	6	33.3 ± 0.96	36.4 ± 0.61	+ (0.01)	+ (0.01)	0	+ (N.S.)	- (N.S.)
	Southdown	HP8-30	6	37.3 ± 0.14	35.9 ± 0.41	- (0.05)	- (0.01)	- (0.001)	- (N.S.)	- (N.S.)
	"	HP30-8	6	36.0 ± 0.37	37.0 ± 0.27	+ (0.05)	+ (0.02)	+ (0.01)	+ (0.05)	+ (N.S.)
	Welsh	HP8-30	6	36.1 ± 0.59	34.9 ± 0.53	- (0.05)	- (0.01)	- (0.01)	- (0.05)	- (N.S.)
FOOT	"	HP30-8	6	35.4 ± 0.26	37.0 ± 0.25	+ (0.01)	+ (0.001)	+ (0.01)	+ (0.05)	- (N.S.)
TEMPERATURE	Southdown	LP8-30	6	37.3 ± 0.35	33.1 ± 0.93	- (0.01)	- (0.001)	- (0.02)	- (N.S.)	- (N.S.)
	"	LP30-8	6	35.1 ± 0.90	36.6 ± 0.25	+ (0.02)	+ (0.001)	+ (0.02)	+ (0.05)	+ (N.S.)
	Welsh	LP8-30	6	36.4 ± 0.40	32.1 ± 0.88	- (0.001)	- (0.001)	- (N.S.)	- (0.05)	- (N.S.)
	"	LP30-8	6	33.8 ± 0.74	36.6 ± 0.34	+ (0.02)	+ (0.01)	+ (0.05)	+ (N.S.)	+ (N.S.)

Differences are either non significant (N.S.) or denoted as the probability of the difference being due to chance.
Note the trend for extremities to be higher after +8 compared to +30°C exposure

at +30°C before cold exposure than those of their contemporaries kept at +30°C whether in the treatment sequence 8-30 or 30-8 (Fig. 13). Similarly in individual sheep within groups, the same difference was consistently shown between first and second cold exposure whether the treatment 30-8 or 8-30 was imposed. Table 18 gives mean ear and foot temperatures at +30°C before 1st and 2nd acute cold exposure. Sheep on high plane nutrition had slightly higher ear and foot temperatures at +30°C than low plane sheep. Combining breed and temperature groups on both exposures this difference was 1.95°C ($P < 0.001$) and 1.09°C ($P < 0.01$), for the ears and feet respectively. The ear temperatures of Southdown sheep were consistently higher than those of Welsh sheep at +30°C ($P < 0.001$ combining nutrition and temperature groups) but no significant differences were apparent between breeds in foot temperatures at this time. The low initial extremity temperatures of the low plane 8-30 sheep on second cold exposure suggests that these sheep were quite near their critical temperature.

As ambient temperature fell from +30°C to 0°C during acute cold exposure ears and feet showed similar vasomotor responses to those seen in the Blackface (Fig. 13). Sheep exposed to +8°C for 2 weeks, whether in the sequence 8-30 or 30-8, showed delayed vasomotor responses as ambient temperature fell from +30°C to 0°C during subsequent acute cold exposure. Their ear and foot temperatures were consequently higher during this time, see also Table 18. The differences were consistently significant in the early stages of exposure only.

Table 19 gives the mean ambient and skin temperatures at the onset of vasoconstriction during first and second acute cold exposures. The ambient temperature and skin temperature at the onset of vasoconstriction in the 8-30 sheep during the initial lowering of ambient temperature from +30 to +8°C

Table 19.

Mean ambient temperature and ear and foot skin temperature at the onset of vasoconstriction in the ears and feet during the initial temperature drop on day 1 and cold exposures on days 16 and 30

Treatment group		n	Extremity	DAY 2 Initial temperature drop		DAY 16 1st cold exposure		DAY 30 2nd cold exposure	
				Ambient Temperature	Skin Temperature	Ambient Temperature	Skin Temperature	Ambient Temperature	Skin Temperature
Southdown	HP8-30	6	Ear	23.7 ± 0.99	35.6 ± 0.49	22.3 ± 0.84	35.9 ± 0.59	27.2 ± 0.87	36.3 ± 0.35
			Foot	21.2 ± 0.34	34.4 ± 0.38	16.7 ± 1.16	33.1 ± 0.40	24.7 ± 1.02	38.4 ± 0.45
"	HP30-8	6	Ear			25.8 ± 0.65	35.8 ± 0.38	21.0 ± 0.77	35.0 ± 0.70
			Foot			23.0 ± 0.52	33.7 ± 0.70	18.3 ± 0.40	33.5 ± 0.40
Welsh	HP8-30	6	Ear	26.2 ± 1.08	34.7 ± 0.81	23.7 ± 1.45	35.8 ± 0.40	28.3 ± 0.67	34.4 ± 0.85
			Foot	21.2 ± 1.74	33.7 ± 0.40	19.2 ± 1.25	33.3 ± 0.64	26.0 ± 0.73	33.3 ± 0.61
"	HP30-8	6	Ear			28.0 ± 0.68	34.8 ± 0.72	24.7 ± 0.71	35.6 ± 0.31
			Foot			24.0 ± 1.44	33.4 ± 0.68	16.2 ± 1.62	32.9 ± 0.63
Southdown	LP8-30	6	Ear	26.8 ± 1.42	33.7 ± 0.37	26.5 ± 0.70	36.4 ± 0.23	29.5 ± 0.34	33.1 ± 0.75
			Foot	24.0 ± 1.15	34.2 ± 0.33	20.3 ± 1.23	34.9 ± 0.20	27.0 ± 0.52	32.1 ± 0.93
"	LP30-8	6	Ear			28.8 ± 0.41	33.4 ± 0.80	25.7 ± 0.95	35.4 ± 0.58
			Foot			26.3 ± 0.56	34.1 ± 0.50	19.0 ± 3.30	33.5 ± 0.85
Welsh	LP8-30	6	Ear	26.5 ± 1.06	34.1 ± 0.95	26.2 ± 1.35	35.5 ± 0.39	29.7 ± 0.33	32.0 ± 0.30
			Foot	24.7 ± 0.80	35.0 ± 0.38	22.2 ± 0.91	33.8 ± 0.54	27.2 ± 0.48	31.5 ± 0.86
"	LP30-8	6	Ear			29.3 ± 0.34	33.1 ± 0.83	26.5 ± 0.79	35.6 ± 0.46
			Foot			26.2 ± 0.70	32.7 ± 0.63	19.0 ± 3.13	33.7 ± 0.45

Skin temperature was that obtaining immediately prior to vasoconstriction

Table 20.

Analyses of variance for the ambient temperature at onset of vasoconstriction in the feet and ears during first and second cold exposures

EARS

Source of variation	df	1st exposure			2nd exposure		
		M.S.	F	P	M.S.	F	P
Breed	1	10.09	2.15	NS	25.52	8.56	<0.01
Nutrition	1	90.75	19.31	<0.001	77.52	26.01	<0.001
Temperature*	1	133.34	28.37	<0.001	212.52	71.32	<0.001
Breed x Nutrition	1	8.33	1.77	NS	11.02	3.70	NS
Breed x Temperature	1	2.07	0.44	NS	7.52	2.52	NS
Nutrition x Temperature	1	4.08	0.87	NS	6.02	2.02	NS
B x N x T	1	0.01	0.00	NS	2.52	0.85	NS
Error	40	4.70			2.98		

FEET

Source of variation	df	1st exposure			2nd exposure		
		M.S.	F	P	M.S.	F	P
Breed	1	20.02	3.07	NS	0.33	0.01	NS
Nutrition	1	111.02	17.05	<.001	36.75	1.91	NS
Temperature*	1	336.02	51.59	<.001	784.08	40.72	<0.001
Breed x Nutrition	1	2.52	0.39	NS	0.78	0.04	NS
Breed x Temperature	1	9.19	1.91	NS	10.08	0.52	NS
Nutrition x Temperature	1	1.02	0.16	NS	0.00	-	NS
B x N x T	1	0.19	0.03	NS	8.33	0.43	NS
Error	40	6.51			19.26		

* during the preceding 2 weeks

on day 2 are also shown. Analyses of variance for ambient temperature at the onset of vasoconstriction in the ears and feet (Table 20) show clearly that previous experience of cold consistently caused delayed vasoconstriction responses. High plane sheep, in general, also vasoconstricted at lower ambient temperatures than low plane sheep. This might be expected from their theoretically lower critical temperature. The small effect of plane of nutrition on vasoconstriction in the feet on second cold exposure appeared to be largely the result of one sheep in each of the Southdown LP30-8 and Welsh LP30-8 groups delaying vasoconstriction until +5°C and +3°C respectively. Within individuals there was generally no strict relationship between the time of vasoconstriction and resistance to cooling, nor between the change in the two parameters after cold exposure. These two sheep did, however, show a greater than average improvement in resistance to cooling. There was no relationship within groups between the ambient temperature of onset of vasoconstriction and bodyweight.

Comparison of the data for the 8-30 groups of sheep during the initial lowering of ambient temperature on day 2 with the 8-30 and 30-8 groups during first cold exposure (day 16) suggests that the ambient temperature threshold for vasoconstriction was affected by exposure to +8°C and by exposure at the thermoneutral temperature +30°C. The ears of 30-8 sheep on day 16 vasoconstricted at a mean ambient temperature 2.9°C ($P < 0.01$) higher than the 8-30 sheep on day 2, whereas vasoconstriction in the 8-30 sheep on day 16 occurred only 1.3°C (N.S.) lower by comparison with their own values on day 2. Similarly, vasoconstriction in the foot occurred 2.1°C ($P < 0.02$) earlier, and 3.3°C ($P < 0.01$) later in the 30-8 and 8-30 sheep respectively on day 16 compared with that in the 8-30 sheep on day 2. The possibility that emotional factors may have contributed to this result

cannot be ruled out, as the sheep would be more used to handling and restraint on day 16. However there was no visible change in the reactions of sheep to restraint or the fixing of equipment between days 2 and 16. The results would otherwise suggest that the 30-8 sheep to some extent adjusted to a warm environment while at 30°C. For example, basal heat production does decrease during acclimatization to heat in cattle (Kibler, Johnson, Shanklin and Hahn, 1965 and Bianca, 1959). But according to the data of Armstrong et al. (1960) +30°C should not have been above thermoneutral, especially for the low plane sheep. Moreover the sheep showed no signs of heat stress and in fact some low plane sheep were slightly vasoconstricted at +30°C (see below).

Vasoconstriction in all treatment groups invariably occurred in the ear before the foot, and this difference tended to be exaggerated following cold exposure (Table 19). On average, vasoconstriction occurred in the ear at an ambient temperature 3.4°C ($P < 0.001$) higher than in the foot, and ear temperature subsequently fell more rapidly than foot temperature, at rates comparable to those shown by the Blackface sheep Fig. 3. There was however a significant relationship within individuals between the ambient temperatures at which vasoconstriction occurred in the ears and feet ($r = +0.64$; $P < 0.001$). Table 19 also gives the mean ear and foot temperature just before vasoconstriction. Ear and foot temperatures at vasoconstriction in the high plane sheep were each very uniform between groups, irrespective of breed and previous temperature treatment. On average, ear temperature at vasoconstriction was 34.9°C, that is 1.6°C ($P < 0.001$) higher than foot temperature at vasoconstriction. The apparent tendency for low plane sheep, especially those in the 8-30 groups, to vasoconstrict at lower skin temperatures after being kept at +30°C

before acute cold exposure than after an equivalent period of time at +8°C was fallacious. Some sheep were in fact showing partial vasoconstriction at +30°C before exposure began. During exposure to +8°C these sheep had shown a considerable loss in bodyweight (Table 27). It seems probable that when returned to +30°C after the first acute cold exposure basal metabolism had returned to normal, and these sheep, on maintenance level of feeding, were just below their critical temperature. In the computation of the ambient temperature of vasoconstriction these sheep were scored +30°C. This would not invalidate the analysis since, if anything, it would reduce the difference between temperature treatment groups.

At sub-zero temperatures cold-induced vasodilatation was observed in the ears, but, as in the Blackface, rarely in the feet. Table 21 gives the frequency of cold-induced vasodilatations during first and second acute cold exposures. There were no significant differences between groups in the number of cold vasodilatations nor between these sheep and the Blackface sheep in 1965/66. Considerable variation was observed between individuals, but there was a tendency, especially in high plane nutrition groups, for the size of cold vasodilatations to increase after prolonged exposure to +8°C ($P < 0.01$ combining all groups). This is a similar trend to that shown earlier by the Blackface sheep. Like the Blackface, the Southdown and Welsh sheep rarely showed the rhythmical patterns of cold vasodilation termed by Lewis (1930) the "hunting reaction".

(b) Before and between acute cold exposures (days 2, 14, 18 and 28)

Table 22 shows mean midside, ear and foot temperatures at the respective treatment temperatures on days 2, 14, 18 and 28. Midside temperatures of the two breeds of sheep were similar, as were those of

Table 21. Cold vasodilatations in the ears at sub-zero temperatures

Treatment group	Mean total no. of vasodilatations per 100 min. exposure				Mean no. of large vasodilatations per 100 min. exposure	
	n	1st exposure	n	2nd exposure	1st exposure	2nd exposure
Southdown HP8-30	6	3.98 ± 0.52	5	2.94 ± 0.52	0.37 ± 0.17	0.25 ± 0.16
Southdown HP30-8	6	2.57 ± 0.59	5	3.44 ± 0.63	0	0.73 ± 0.31
Welsh HP8-30	5	3.31 ± 0.86	5	1.93 ± 0.41	0.89 ± 0.57	0
Welsh HP30-8	6	3.12 ± 0.32	5	4.06 ± 1.31	0.08 ± 0.08	0.57 ± 0.42
Southdown LP8-30	5	2.89 ± 0.63	6	3.55 ± 0.35	0.58 ± 0.24	0.19 ± 0.14
Southdown LP30-8	6	4.56 ± 1.04	5	3.51 ± 0.52	0.50 ± 0.32	0.70 ± 0.27
Welsh LP8-30	5	5.33 ± 0.43	6	4.10 ± 0.51	1.07 ± 0.31	0
Welsh LP30-8	6	4.40 ± 0.84	6	4.30 ± 0.46	0.75 ± 0.38	0.61 ± 0.39

Vasodilatations were defined as temporary fluctuations in skin temperature greater than 1.5°C or, for large vasodilatations, greater than 10°C.

Fewer than 6 individuals appear in some groups since some thermocouples were broken during exposure.

Table 22. Mean skin temperatures (°C) on the midside, ear and foot on days 2, 14, 18 and 28 at the respective treatment temperatures

		Midside temperature				Ear temperature				Foot temperature			
Treatment group	n	Day 2	14	18	28	2	14	18	28	2	14	18	28
Southdown HP8-30	6	27.1 ± 0.26	27.7 ± 0.57	36.5 ± 0.21	36.1 ± 0.25	12.3 ± 0.53	13.2 ± 0.41	38.3 ± 0.11	37.8 ± 0.30	14.6 ± 0.47	10.9 ± 0.40	37.3 ± 0.17	36.9 ± 0.34
Southdown HP30-8	6	36.4 ± 0.24	36.7 ± 0.14	26.8 ± 0.68	27.4 ± 0.44	37.2 ± 0.38	38.1 ± 0.14	13.1 ± 1.02	12.8 ± 1.38	36.2 ± 0.36	36.6 ± 0.35	12.7 ± 0.38	12.5 ± 1.78
Welsh HP8-30	6	27.2 ± 0.72	26.3 ± 0.88	37.0 ± 0.09	36.4 ± 0.26	10.6 ± 0.44	11.47 ± 0.48	37.9 ± 0.31	36.5 ± 0.56	13.4 ± 0.44	11.2 ± 1.21	37.1 ± 0.28	35.70 ± 0.45
Welsh HP30-8	6	36.8 ± 0.36	36.8 ± 0.33	27.7 ± 0.69	27.5 ± 0.71	36.6 ± 0.61	36.2 ± 0.92	12.9 ± 1.24	11.7 ± 0.25	35.9 ± 0.41	36.2 ± 0.30	14.1 ± 3.02	10.1 ± 0.62
Southdown LP8-30	6	29.5 ± 0.72	29.2 ± 0.58	37.0 ± 0.33	36.7 ± 0.19	11.7 ± 0.64	13.9 ± 1.97	38.2 ± 0.27	34.8 ± 0.93	13.3 ± 0.49	10.6 ± 0.31	37.2 ± 0.36	34.2 ± 0.78
Southdown LP30-8	6	37.0 ± 0.12	36.7 ± 0.10	28.7 ± 0.72	28.7 ± 0.46	36.0 ± 0.94	36.4 ± 0.69	12.5 ± 0.97	13.0 ± 0.74	36.4 ± 0.36	35.9 ± 0.53	14.0 ± 2.61	10.2 ± 0.13
Welsh LP8-30	6	29.0 ± 0.55	29.9 ± 0.45	37.3 ± 0.26	36.7 ± 0.17	12.0 ± 0.42	12.6 ± 1.91	38.2 ± 0.11	35.6 ± 0.60	13.0 ± 0.38	12.0 ± 1.90	36.7 ± 0.42	34.2 ± 0.53
Welsh LP30-8	6	36.9 ± 0.10	36.8 ± 0.11	29.2 ± 0.56	28.2 ± 0.41	35.6 ± 0.75	36.7 ± 0.50	11.2 ± 0.39	15.3 ± 3.23	34.7 ± 0.54	34.7 ± 0.57	14.3 ± 1.41	13.6 ± 2.59

For 8-30 sheep ambient temperature was +8°C on days 2 and 14 and +30°C on days 18 and 28.

For 30-8 sheep ambient temperature was +30°C on days 2 and 14 and +8°C on days 18 and 28.

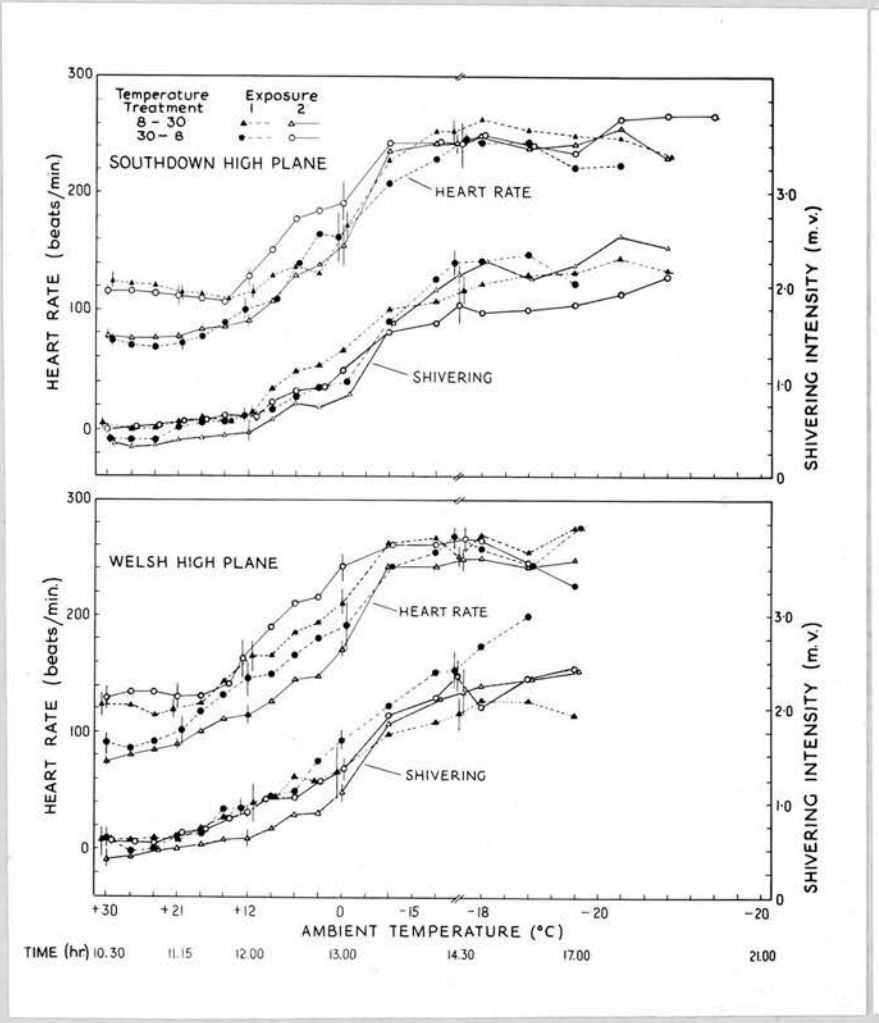
sheep on high and low plane nutrition when measured at +30°C. At +8°C, however, low plane sheep of both breeds had slightly higher midside temperatures than high plane sheep. Over all groups the difference was 1.82°C ($P < 0.001$). This may have been due to high plane sheep possessing greater tissue insulation, possibly as a result of larger deposits of subcutaneous fat. However, no consistent relationship could be demonstrated between skinfold thickness and midside temperature within groups of sheep, nor was there any significant relationship over all groups of sheep.

There were no consistent differences in ear or foot temperatures due to breed or plane of nutrition, nor between these and the Blackface sheep measured at the same ambient temperature. There was no evidence for relaxation of vasoconstriction after prolonged cold exposure. Occasional high values were the result of one or two sheep exhibiting vasodilatation at +8°C. These were apparently random. The low foot and ear temperatures of the low plane 8-30 sheep at +30°C on day 28 support the previous conclusions regarding the critical temperature of these sheep.

3. Heart rate

(a) During acute cold exposure (days 16 and 30)

Fig. 14 shows mean heart rates during first and second acute cold exposures. Responses were similar to those of the Blackface sheep in 1965/66. Whether in the sequence 8-30 or 30-8 the effect of chronic exposure to +8°C was to increase heart rates when measured at +30°C before the subsequent acute cold exposure. Heart rates were, on average, 50% higher following 2 weeks at +8°C. Analyses of variance for heart rate



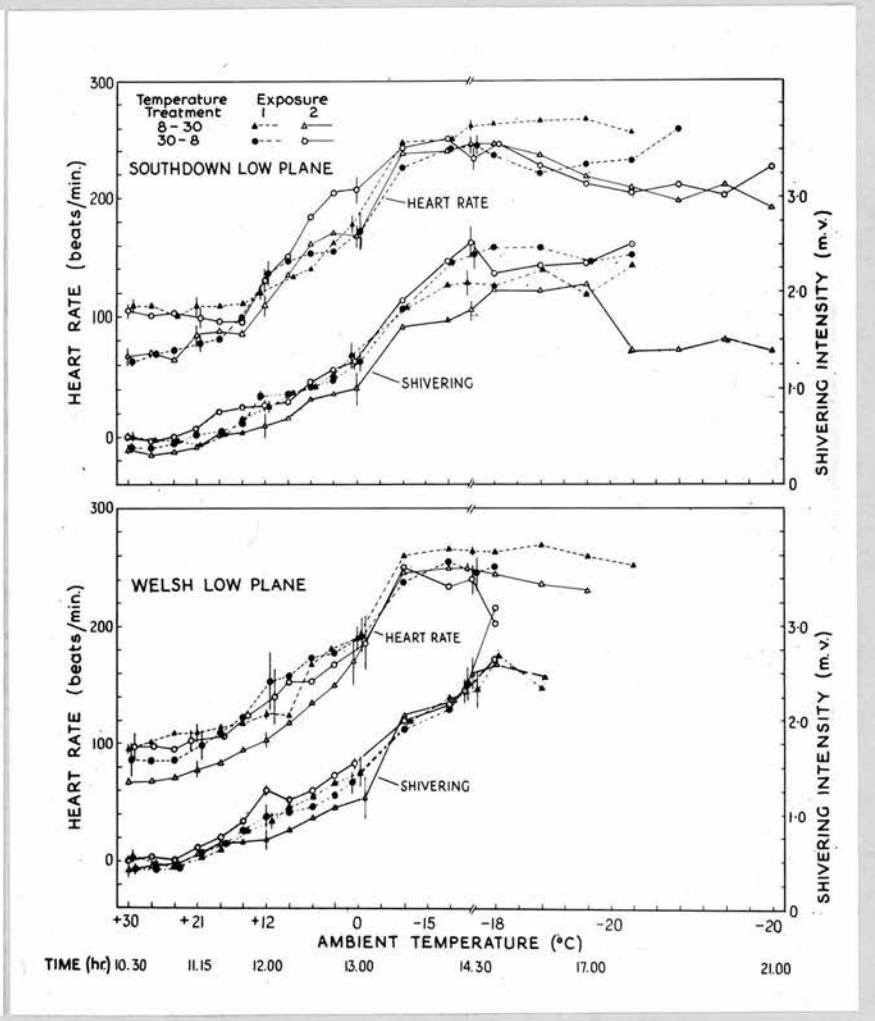


Fig. 14. The changes in mean heart rate and shivering intensity of high and low plane Southdown and Welsh sheep in the 8-30 and 30-8 temperature treatment groups during first and second cold exposures.

There were 6 sheep per group. Ambient temperature was lowered progressively according to the time scale shown.

Table 23. Analyses of variance for heart rate at +30°C (10.30 hrs.) before 1st and 2nd cold exposures

Source of variation	df.	1st exposure			2nd exposure		
		M.S.	F	P	M.S.	F	P
Breed	1	432.00	0.95	NS	13.02	0.05	NS
Nutrition	1	2552.08	5.63	<0.05	3088.02	11.54	<0.01
Temperature	1	14910.75	32.00	<0.001	18841.69	70.38	<0.001
Breed x Nutrition	1	0.34	0.00	NS	212.52	0.79	NS
Breed x Temperature	1	2080.33	4.59	<0.05	63.02	0.24	NS
Nutrition x Temperature	1	752.09	1.66	NS	450.18	1.68	NS
B x N x T	1	191.99	0.42	NS	379.69	1.42	NS
Error	40	453.29			267.70		

at +30°C before 1st and 2nd acute cold exposures, Table 23, show clearly the effects of previous temperature treatment. Also, high plane sheep had slightly higher heart rates than low plane sheep. Riek, Hardy, Lee and Carter (1951) have shown a similar effect of nutrition. The interaction between breed and temperature treatment shown on first exposure appeared to be caused by two Welsh LP30-8 sheep having rather high heart rates, while one sheep in each of the Welsh HP8-30 and LP8-30 had abnormally low heart rates. The uniformity of response on second exposure suggests that these were probably chance effects.

Heart rates of sheep previously kept at +30°C began to increase gradually between +29°C and +21°C during acute cold exposure. Those of sheep previously kept at +8°C however, with the exception of the low plane Welsh groups, remained fairly steady until 24-15°C when they began to increase at a similar rate. Heart rates of all groups of sheep were similar at sub-zero temperatures. Although sheep in groups previously kept at +8°C had higher heart rates at +30°C and also showed an improvement in subsequent performance, there was no relationship between the two parameters within individuals. Similarly, heart rate during sub-zero exposure was apparently not related to resistance to cooling.

(b) Before and between acute cold exposures (days 2, 14, 18 and 28)

Fig. 15 shows mean heart rates of the 8 groups of sheep on six occasions; after the sheep had remained undisturbed for 1½ hours at +30°C before the first and second cold exposures (i.e. on days 16 and 30) and between 10.30 hrs. and 14.30 hrs. on days 2, 14, 18 and 28 at the treatment temperatures of +30°C and +8°C. There was no consistent difference between breeds in heart rate on any occasion, but those of high plane sheep were

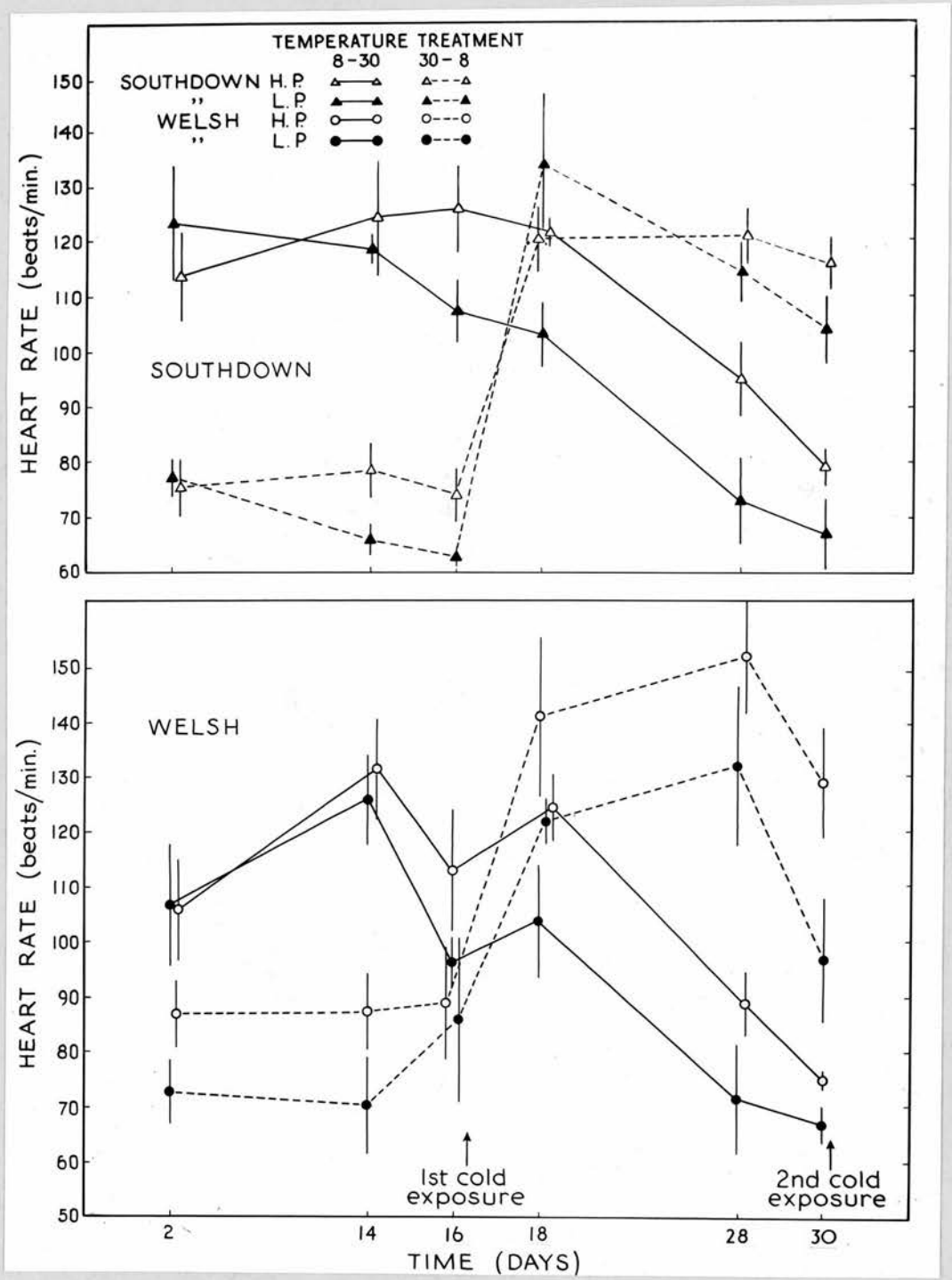


Fig. 15. Mean heart rates in the eight treatment groups (6 sheep per group) before and between acute cold exposures.

On days 16 and 30 the ambient temperature was +30°C for all sheep; on days 2 and 14 the ambient temperatures were +8°C and +30°C according to the temperature treatment imposed, while on days 18 and 28 those temperatures were reversed.

again generally higher than those of comparable low plane sheep, especially in the Welsh breed. Heart rates of all sheep at +8°C were significantly higher than those of comparable sheep at +30°C on days 2 and 14 ($P < 0.001$ in all cases). On day 18, two days after acute cold exposure, heart rates of sheep at +8°C were only slightly higher than those of sheep at +30°C. But by day 28 the heart rates of sheep at +30°C had fallen, so that at this time the difference between the two temperature groups was again highly significant ($P < 0.001$ for high and low plane). It appears, therefore, that basal metabolic rates, measured at +30°C, were elevated as a result of previous chronic exposure to +8°C. The effects were consistent and apparently easily reversible within the time scale of the experiment. The data suggest that acute cold exposure may also have caused some elevation of basal metabolism, especially in the Welsh sheep (compare days 18 and 16).

Heart rates of the present sheep when measured at rest in a thermoneutral environment before any cold experience (30-8 sheep on days 2 and 14) were generally between 65 and 90 beats/min. Those of the strictly comparable Blackface sheep (habituation control sheep on days 2 and 14) were similar. These values are in general agreement with the findings of Blaxter (1948), Riek, Hardy, Lee and Carter (1951) and Wodzicka-Tomaszewska and Walmsley (1966) who found resting values to be in the region of 70 beats/min.

(c) Emotional effects

Heart rates fell appreciably between the time that equipment was fixed at 09.00 hrs. and recordings began at 10.30 hrs. However between 10.30 hrs. and 12.30 hrs. on constant temperature days when measurements were made at +30°C, heart rates fell by only 7 beats/min. ($P < 0.05$). These and the observed changes in rectal temperature would suggest that

the effects of emotional disturbance had largely subsided when measurements began at 10.30 hrs. before acute cold exposures.

4. Shivering intensity

(a) During acute cold exposure (days 16 and 30)

Fig. 14 shows mean shivering intensity during first and second acute cold exposures. There was no difference between groups in the temperature of onset of shivering, nor any change within groups as a result of previous temperature treatment. Mean ambient temperature at the onset of shivering was 17.1 $\pm$ 0.48°C for all sheep. Also, during acute cold exposure shivering intensity of the 8 groups was generally similar. However sheep in the temperature sequence 8-30 did tend to show a less rapid initial increase in shivering intensity on second cold exposure, after 2 weeks at +30°C. This is difficult to explain. It may have been due to chance, though the fact that it was shown in all the breed x nutrition groups would tell against this. If, on the other hand, it was related to the degree of cold experience, or the retention of acclimatization gained at the first acute exposure, one would expect to see the same or a larger effect in the 30-8 sheep on second exposure. Possibly the ability of the sheep to respond to the first acute cold exposure had been enhanced by prolonged exposure to chronic moderate cold.

At +30°C before acute cold exposure, sheep which had been kept at +8°C during the previous 2 weeks (whether in the sequence 8-30 or 30-8) showed greater muscle activity on the oscilloscope, while standing perfectly still and showing no signs of shivering. Over all groups the difference was highly significant ($P < 0.001$). This suggests that muscular tone in these

sheep had increased as a result of an increase in the uncoordinated firing of muscle units, as discussed by Burton and Edholm (1955). Swift (1932) demonstrated that increased muscular tone, whether cold induced or voluntarily induced, was accompanied by a considerable increase in metabolism. It seems possible that in these sheep, the apparent increase in basal metabolism, (see heart rate, rectal and skin temperatures) may have been a direct result of increased 'muscle tone', but there was no consistent relationship between these parameters within individuals. However, as in the Blackface data, heart rate and shivering intensity during acute cold exposure were closely correlated. Pairing all recordings of heart rate and shivering intensity between 10.30 hrs. and 13.00 hrs. individual within group correlation coefficients from first exposure ranged from +0.65 to +0.92 ($P < 0.001$ in all cases). If individual variation was reduced by using the group means for shivering and heart rate, the coefficients $r = +0.68$, and $r = +0.87$ ($P < 0.001$ in both cases) were obtained for groups kept at +8°C and +30°C respectively before first exposure. The lower correlation found after chronic cold exposure resulted from the fact that while the increase in heart rate of these sheep was delayed during subsequent acute cold exposure, the onset of shivering was not. There appears to be no ready explanation for this unless, at the time that shivering commenced, there was some reduction in non-shivering thermogenesis.

(b) Before and between acute cold exposures (days 2, 14, 18 and 28)

Table 24 gives mean muscle electrical activity on days 2, 14 18 and 28. Shivering was never observed in sheep kept at +30°C and mean muscle activity of all groups was similar. Sheep kept at +8°C shivered considerably throughout the 2 weeks, and muscle activity was significantly

Table 24. Mean muscle electrical activity (mv) on days 2, 14, 18 and 28

Treatment group	n	Day 2	Day 14	Day 18	Day 28
Southdown HP8-30	6	0.65 ± 0.025	0.70 ± 0.041	0.46 ± 0.030	0.47 ± 0.024
Southdown HP30-8	6	0.46 ± 0.018	0.47 ± 0.026	0.77 ± 0.076	0.68 ± 0.049
Welsh HP8-30	6	0.77 ± 0.046	0.88 ± 0.055	0.44 ± 0.021	0.48 ± 0.026
Welsh HP30-8	6	0.48 ± 0.043	0.53 ± 0.063	0.86 ± 0.078	0.90 ± 0.091
Southdown LP8-30	6	0.77 ± 0.099	0.90 ± 0.070	0.47 ± 0.032	0.46 ± 0.021
Southdown LP30-8	6	0.44 ± 0.026	0.39 ± 0.022	0.75 ± 0.044	0.75 ± 0.032
Welsh LP8-30	6	0.91 ± 0.089	1.26 ± 0.133	0.49 ± 0.029	0.44 ± 0.012
Welsh LP30-8	6	0.42 ± 0.018	0.40 ± 0.019	0.88 ± 0.069	0.92 ± 0.056

For 8-30 sheep ambient temperature was +8°C on days 2 and 14 and +30°C on days 18 and 28
For 30-8 sheep ambient temperature was +30°C on days 2 and 14 and +8°C on days 18 and 28

($P < 0.001$) greater than in sheep kept at +30°C during this time. At +8°C muscle activity of the Welsh sheep was greater than that of the Southdowns. Combining measurements on days 2, 14, 18 and 28, this was significant on both high and low plane nutrition ($P < 0.02$ and < 0.01 respectively).

Although the sheep appeared to become more comfortable during their stay at +8°C, in that they gradually spent more of the time lying down and adopted less hunched postures, there was no observed decrease in shivering intensity as would be expected if shivering thermogenesis was being replaced by non-shivering thermogenesis.

5. Respiration rate

(a) During acute cold exposure (days 2 and 16)

Fig. 16 gives the mean respiration rates during acute cold exposure. Changes in respiration rate were similar to those shown by the Blackface sheep in 1965-66, and they were not affected by previous temperature treatment. At +30°C, before cold exposure began, high plane sheep had higher respiration rates than low plane sheep ($P < 0.001$). On low plane nutrition there was no difference between breeds, but on high plane nutrition the rates for Southdown sheep were higher than for the Welsh ($P < 0.02$). As ambient temperature fell from +30°C the respiration rates of high plane sheep fell, so that at +18°C the rates for all sheep were similar. As in the Blackface sheep, respiration rate increased as the environment became very cold. Between +18°C (11.30 hrs.) and -16°C (14.30 hrs.) the rate increased from 24 to 37/min., ($P < 0.001$). An assessment of tidal volume was made in a similar way to that described for the Blackface sheep. There were

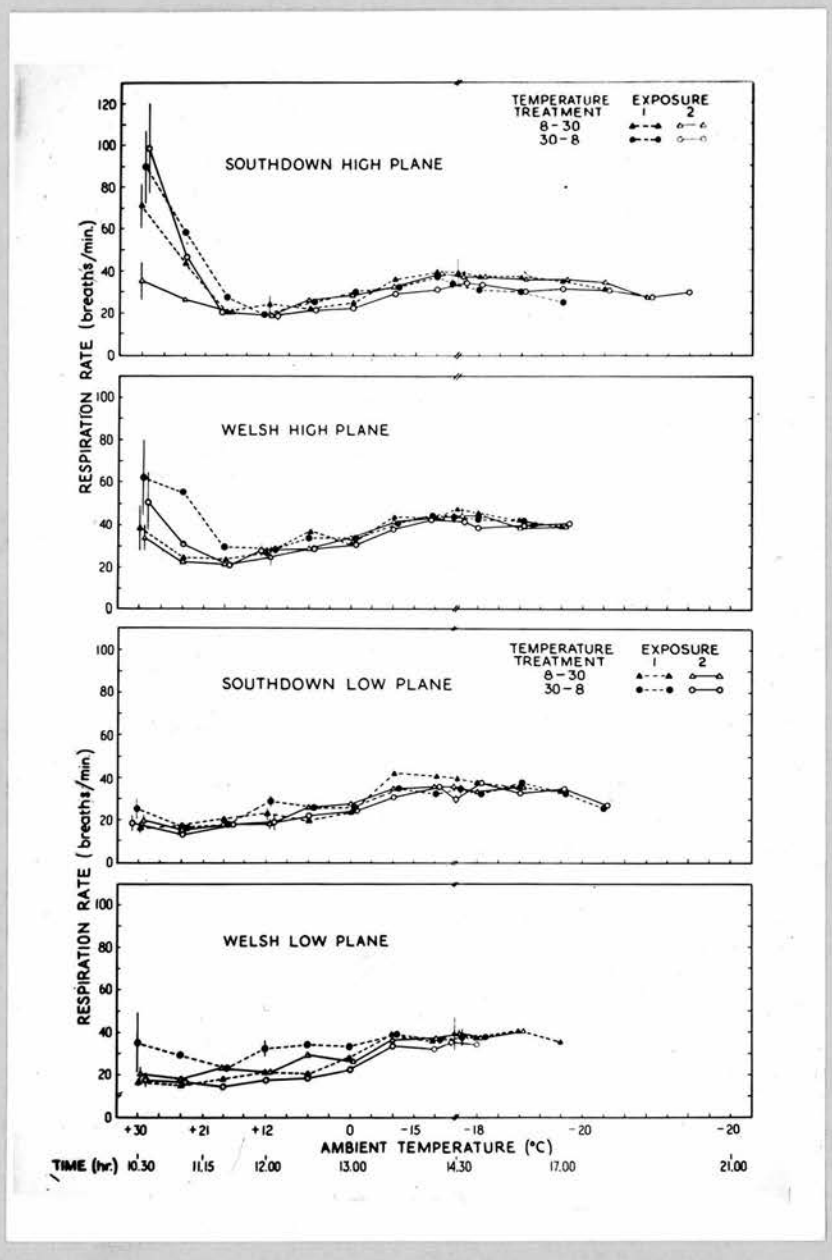


Fig. 16. The changes in mean respiration rate in the high and low plane Southdown and Welsh sheep in the 8-30 and 30-8 temperature treatment groups during first and second cold exposure.

Ambient temperature was lowered progressively according to the time scale shown.

Table 25 (a) Mean tidal volume* during 1st and 2nd acute cold exposures

Treatment group	n	1st Exposure			2nd Exposure		
		+30°C(10.30hrs.)	+18°C(11.30hrs.)	-16°C(14.30hrs.)	+30°C(10.30hrs.)	+18°C(11.30hrs.)	-16°C(14.30hrs.)
8-30	24	0.66 ± 0.083	1.21 ± 0.094	2.01 ± 0.171	0.40 ± 0.037	0.98 ± 0.091	1.57 ± 0.105
30-8	24	0.45 ± 0.048	1.22 ± 0.100	1.68 ± 0.119	0.42 ± 0.054	1.13 ± 0.109	1.65 ± 0.142

Table 25 (b) Mean tidal volume* on days 2, 14, 18 and 28

Treatment group	n	Day 2	Day 14	Day 18	Day 28
8-30	24	1.09 ± 0.097	1.33 ± 0.122	0.59 ± 0.064	0.52 ± 0.050
30-8	24	0.58 ± 0.062	0.54 ± 0.074	1.36 ± 0.198	1.51 ± 0.252

* Tidal volumes were estimated from averaged kymograph trace amplitudes.

High and low plane nutritional groups were combined in both tables.

In Table 25(b) - ambient temperature for 8-30 sheep was +8°C on days 2 and 14 and +30°C on days 18 and 28.
ambient temperature for 30-8 sheep was +30°C on days 2 and 14 and +8°C on days 18 and 28.

no differences between groups due to plane of nutrition or breed and the data have therefore been presented only for the temperature treatment groups. 'Tidal volumes' of all groups of sheep (Table 25a) showed similar gradual increases during cold exposure, and were not affected by previous temperature treatment.

(b) Before and between acute cold exposures (days 2, 14, 18 and 28)

Table 26 shows the mean respiration rates between 10.30 hrs. and 14.30 hrs. on days 2, 14, 18 and 28. There were no differences due to breed or plane of nutrition at +8°C. However, at +30°C, respiration rates of high plane sheep were consistently higher than those of corresponding low plane sheep ($P < 0.001$ over all groups), while on high plane nutrition there was a tendency for Southdown sheep to exhibit higher rates than Welsh. These differences were similar to those at +30°C before cold exposure. Although sheep at +8°C had lower respiration rates than sheep at +30°C they showed greater tidal volumes (Table 25b). The trend for the depth of respiration to increase with prolonged cold exposure was non-significant. These responses were similar to those previously observed in the Blackface sheep.

The lability of respiration rate at high environmental temperatures as part of the heat dissipation mechanism of animals is well established in sheep (Blaxter et al., 1959; Bligh, 1963), and in cattle (Findlay, 1957; Bianca, 1966). Changes in respiration rate with ambient temperature followed a similar pattern to those described by Blaxter et al. (1959). The higher respiration rates of high plane sheep, especially the larger Southdowns, at +30°C probably reflected a higher metabolic rate, and therefore the need for heat dissipation. However, comparison of these values with the

Table 26. Mean respiration rates on days 2, 14, 18 and 28

Treatment group	n	Day 2	Day 14	Day 18	Day 28
Southdown HP8-30	6	23.7 ± 1.67	18.3 ± 1.40	127.9 ± 3.01	93.1 ± 7.57
Southdown HP30-8	6	117.5 ± 7.83	106.4 ± 11.15	20.2 ± 0.91	16.5 ± 1.20
Welsh HP8-30	6	29.2 ± 3.88	20.6 ± 0.45	107.0 ± 9.87	79.0 ± 7.78
Welsh HP30-8	6	67.4 ± 10.55	107.9 ± 12.81	23.1 ± 1.85	24.0 ± 1.86
Southdown LP8-30	6	25.2 ± 3.14	20.0 ± 1.76	41.1 ± 8.30	30.4 ± 3.60
Southdown LP30-8	6	40.1 ± 6.31	46.7 ± 7.39	18.8 ± 1.27	16.7 ± 2.21
Welsh LP8-30	6	21.8 ± 1.68	20.0 ± 1.15	36.0 ± 8.51	27.6 ± 3.80
Welsh LP30-8	6	28.3 ± 4.65	44.2 ± 7.31	20.3 ± 1.53	17.4 ± 1.54

For 8-30 sheep ambient temperature was +8°C on days 2 and 14 and +30°C on days 18 and 28.
For 30-8 sheep ambient temperature was +30°C on days 2 and 14 and +8°C on days 18 and 28.

data of Blaxter et al. (1959) on changes in respiration rate and metabolic rate with ambient temperature, suggests that the choice of +30°C as a thermo-neutral temperature was a good compromise. Low plane sheep were probably just at their critical temperature, while high plane sheep were not subjected to thermal stress. Increased tidal volumes on cold exposure coupled with a decrease in respiration rate, have been demonstrated previously in sheep by Joyce and Blaxter (1964b). The slight increase in respiration rate observed below the critical temperature in the present experiment may have been associated with the need to increase oxygen consumption rapidly to maintain very high metabolic rates. In general, though, respiration responded to changes in temperature in a manner predictable from its role as a defence mechanism against heat. There was no evidence to suggest that it was modified during acclimatization to cold.

6. Bodyweight and Food Consumption

Table 27 gives the mean bodyweights before and during experimental treatment. The low plane ration maintained bodyweight fairly constant until temperature treatment began, while the high plane ration allowed an average increase in bodyweight of 42% during this time.

Between days 1 and 15, low plane sheep kept at +30°C showed no change in bodyweight, while those at +8°C showed a significant loss ($P < 0.001$, combining breed groups). Between days 15 and 29, exposure to +8°C again caused a significant loss of bodyweight ($P < 0.001$, combining breed groups) while sheep at +30°C during this time showed a slight though non-significant recovery. Only one of the 24 low plane sheep refused a small quantity of food while in the chamber.

High plane sheep kept at +8°C suffered a considerable loss of bodyweight,

Table 27. Mean bodyweights (kg.)

Treatment group	n	October 5th* 1966	Day 1+	Day 15+	Day 29+
Southdown HP8-30	6	23.6 ± 0.80	34.0 ± 2.31	30.9 ± 2.08	32.2 ± 2.09
Southdown HP30-8	6	24.2 ± 0.63	35.5 ± 2.22	32.8 ± 1.53	31.4 ± 1.65
Welsh HP8-30	6	20.1 ± 0.50	28.2 ± 2.65	26.3 ± 1.07	27.3 ± 1.66
Welsh HP30-8	6	20.0 ± 0.62	27.5 ± 1.83	26.3 ± 1.07	24.8 ± 1.05
Southdown LP8-30	6	23.8 ± 0.66	24.9 ± 0.66	21.9 ± 0.61	23.4 ± 0.69
Southdown LP30-8	6	24.2 ± 0.60	25.8 ± 0.36	25.6 ± 0.35	22.8 ± 0.36
Welsh LP8-30	6	20.0 ± 0.39	19.9 ± 0.57	17.8 ± 0.37	18.3 ± 0.34
Welsh LP30-8	6	19.8 ± 0.36	19.2 ± 0.51	19.3 ± 0.77	17.8 ± 0.53

* Sheep were in full fleece

+ Sheep were shorn.

whether exposed between days 1 and 15 or days 15 and 29 ($P < 0.001$ in both cases). However, sheep kept at +30°C between days 1 and 15 also lost weight ($P < 0.05$). The changes in bodyweight of both groups were undoubtedly influenced by food refusals which were common on high plane nutrition, Fig. 17. Considerable variation was observed between individuals with the result that differences between groups did not achieve statistical significance, but they seemed worthy of discussion. In general Welsh sheep refused more food than Southdowns, while sheep in the cold tended to refuse more than when in the warm. Although the Welsh HP30-8 sheep were rather exceptional, food refusals in the cold tended to be maximal initially and to decline thereafter. The apparently large reduction in food refusals shown by the 8-30 sheep on return to +30°C after 2 weeks at +8°C may merely have been the result of habituation to the climate chamber environment. But little evidence for this was seen in the 30-8 groups while at +30°C. Weiss (1958) measured the feed intake of mice following daily exposure to -3°C for 20 min. Intake was depressed initially before increasing to levels greater than in the controls. The maximum feed intake of the sheep was not tested, but intake did tend to recover after being initially depressed, apparently by cold. Increases in the feed intake of sheep have been found after shearing (Wheeler, Reardon and Lambourne, 1963; Wodzicka-Tomaszewska, 1964) which can be considered to impose some degree of cold stress. However Webster and Lynch (1966) although reaching similar conclusions did find evidence for an initial depression of intake and also found that on cold nights sheep did not eat while shivering. Overnight temperature in some instances reached +5°C, i.e. 3°C lower than that used to induce acclimatization in the present experiment. It seems possible that while mild cold exposure, as experienced after shearing in normal conditions

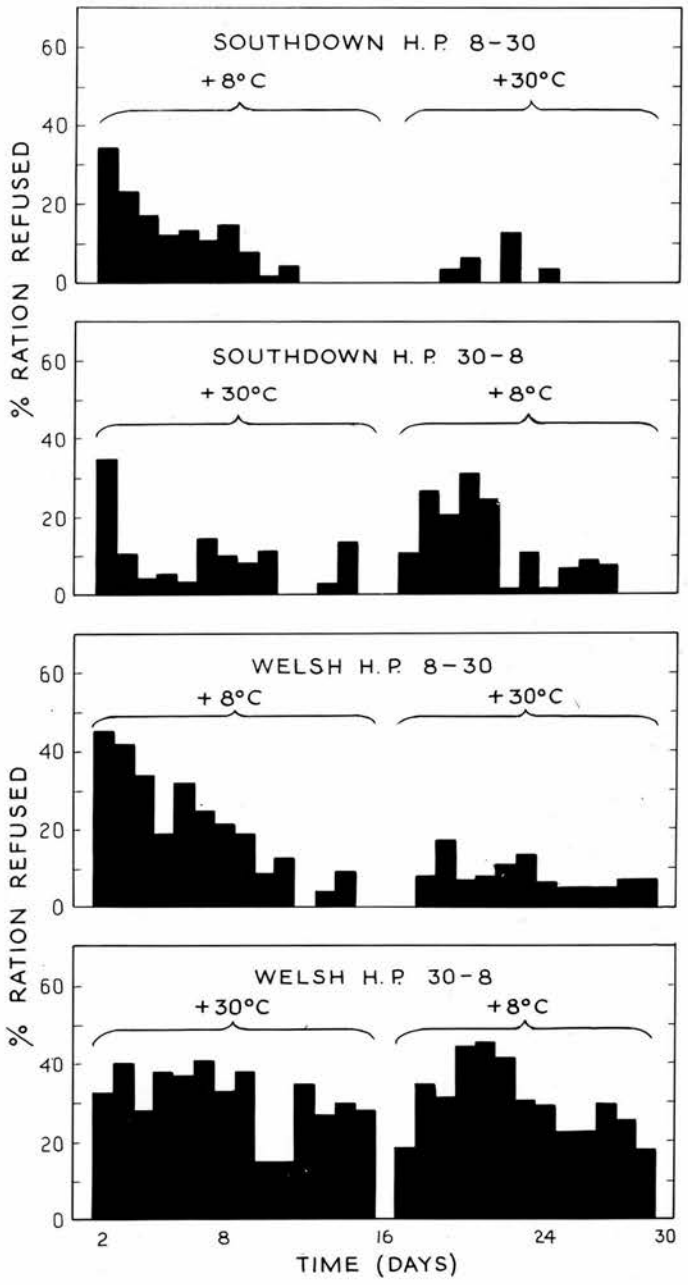


Fig. 17. The food refusals of high plane Southdown and Welsh sheep in the 8-30 and 30-8 temperature treatment groups before and between acute cold exposures.

can stimulate food intake, really severe exposure can reduce intake presumably by causing discomfort. The trend for food intake to return to normal may reflect a reduction in discomfort as a result of acclimatization, though there was little outward sign of this.

An interesting feature of the data was that low plane sheep losing a considerable amount of bodyweight (up to 20%) could still show improved resistance to cooling as a result of acclimatization. There was however no relationship between bodyweight loss or the amount of food refused and subsequent performance. Moreover, although Southdown sheep had generally greater resistance to body cooling than Welsh sheep, no significant relationship could be found between resistance to cooling and bodyweight.

7. Skinfold thickness

Fig. 18 shows the changes in mean skinfold thickness of the 8 treatment groups measured on days 1, 15 and 29, and those of six Southdown and six Welsh control sheep, 3 on high and 3 on low plane nutrition, which were measured at the same times. The controls were unshorn and remained undisturbed in the indoor sheep pens between measurements. Analysis of variance showed that Southdown sheep had a greater skinfold thickness than Welsh sheep on day 1 ($P < 0.01$) but there was no effect of plane of nutrition. By day 15, those sheep kept at +8°C had shown a 30% increase in thickness while no change had occurred in sheep kept at +30°C or in the control sheep. Analysis of variance for skinfold thickness on day 15 showed a highly significant effect of temperature treatment, ($P < 0.001$). The breed effect, which was apparent on day 1, had diminished as a result of the Welsh sheep showing a slightly greater increase in skinfold thickness than the Southdowns. A similar effect of cold exposure was seen in the 30-8

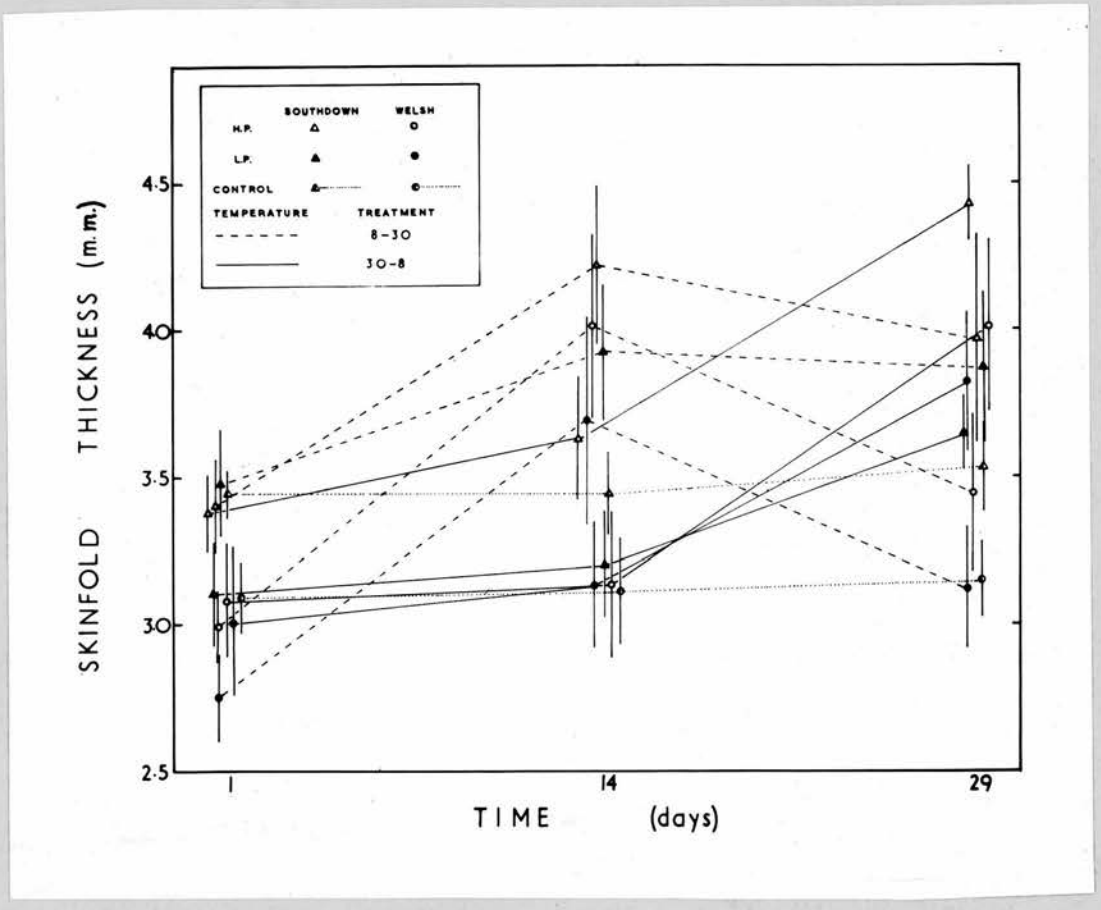


Fig. 18. Mean skinfold thickness in the eight treatment groups (6 sheep per group) on days 1, 14 and 29.

Between days 1 and 14 ambient temperature was +30°C or +8°C according to the treatment imposed on the group, while between days 18 and 28 these temperatures were reversed. The values for control sheep, which were kept unshorn in indoor pens during the same time period, are also shown.

sheep when the temperature treatments were reversed (days 15-29), while skinfold thickness of the 8-30 sheep (especially the Welsh) tended to decline slightly during this time. There was no relationship between skinfold thickness and performance. Skinfold thickness of the Blackface sheep, though initially greater than that of the Southdowns and Welsh, showed slightly smaller changes on cold exposure.

Wodzicka-Tomaszewska (1960a) demonstrated increases in skinfold thickness of sheep during cold exposure. Her sheep, 4 Merinos and 2 Southdowns, had an initial skinfold thickness of 2.4 mm and showed a maximal increase of 50% after 14 days. By comparison, the present sheep had a greater initial skinfold thickness but showed only a 20-30% increase during the same period of time.

8. Subsidiary treatment group

The data in Tables 3a and 15 show that the three breeds of sheep could be ranked in the order Blackface, Southdown and Welsh for resistance to body cooling before cold experience. Moreover Blackface sheep, Table 3a also showed the greatest capacity to acclimatize to cold. Data from Blackface sheep subjected to the same sequence of temperature treatment as the Southdown and Welsh sheep (i.e. the high and low plane habituation control sheep, Table 13) suggested, by comparison with the main treatment groups on first exposure (Table 3a) that restraint in the climate chambers at +30°C for two weeks may have had a deleterious effect on subsequent performance. It was therefore considered important to establish whether the apparent difference in cooling resistance between the Blackface and the Southdown and Welsh sheep could have been partially caused by the modified sequence of treatment. A further twelve Welsh and Southdown sheep (3 high plane and

Table 28.

Resistance to body cooling, ambient temperature and skin temperature at onset of vasoconstriction, heart rate and bodyweights of the subsidiary treatment groups at first acute cold exposure - Southdown and Welsh sheep

Parameter	Southdown		Welsh	
	High Plane	Low Plane	High Plane	Low Plane
Rate of fall of body temperature (°C/100 min. from 0°C-13.00 hrs.)	0.834 ± 0.151	1.223 ± 0.086	1.124 ± 0.048	3.656 ± 0.862
Ambient temperature at ear vasoconstriction	30.0 ± 0	28.6 ± 0.39	28.6 ± 0.39	30.0 ± 0
*Ear temperature	34.5 ± 0.96	31.7 ± 0.13	33.7 ± 0.67	32.2 ± 0.17
Ambient temperature at foot vasoconstriction	26.5 ± 0.50	25.7 ± 0.88	24.7 ± 1.20	27.6 ± 0.39
*Foot temperature	35.3 ± 0.20	32.4 ± 0.67	34.3 ± 0.32	33.0 ± 1.50
Mean heart rate at +30°C (10.30 hrs.) (Beats/min.)	76.0 ± 7.02	83.3 ± 12.66	85.3 ± 5.33	66.3 ± 4.26
Mean body weight (kg.)	48.7 ± 0.62	31.7 ± 0.73	35.9 ± 1.52	18.9 ± 1.18

* Ear and foot temperatures were those obtaining immediately prior to vasoconstriction

3 low plane of each breed) were therefore cold-exposed after only 18 hrs. in the climate chambers, according to the precedure used for the HP8 and LP8 Blackface sheep in 1965/66. The mean rates of body cooling (Table 28) were not significantly different from those of the main treatment groups. The sheep, with the exception of the low plane Welsh, were heavier than the main treatment groups, and although there was only a poor relationship between bodyweight and resistance to cooling, it seems probable that if adjusted for bodyweight their performance may have been slightly inferior. This was therefore strong confirmatory evidence in favour of a real breed difference in cold resistance between the Southdown, Welsh and Blackface breeds.

The vasomotor responses of these sheep tended to occur at a relatively high ambient temperature, when compared to those of sheep in the main treatment groups. It may be significant that the two weeks prior cold exposure of these sheep had coincided with unusually warm weather during which the temperature in the holding pens reached 25°C for a few hours each day. Blaxter (1962) gives the critical temperature of well fed sheep in full fleece as below 0°C, so that these sheep, especially the heavy high plane, may have been under some degree of heat stress. Bianca (1959) and Kibler, Johnson, Shanklin and Hahn (1965) have found evidence for a lowering of metabolic rate during acclimatization of cattle to heat. The possibility that this may have occurred in these sheep cannot be excluded, but the small numbers involved and absence of confirmatory evidence in the heart rates make it unwise to speculate further.

9. Vasoconstriction, metabolic responses and the critical temperature

Under the normal terms of definition, the critical temperature is the

highest environmental temperature at which an animal is obliged to increase metabolic rate above the basal level in order to maintain body temperature. It is generally considered that insulative vasomotor responses precede or occur close to the metabolic response (Webster and Blaxter, 1966; Mount, 1964a). The present data showed that there was no strict relationship between the ambient temperatures at which heart rates began to increase, vasoconstriction occurred and shivering commenced. In 131 out of 175 individual exposures including the Blackface, Southdown and Welsh data the increase in heart rate occurred after both ear and foot had vasoconstricted, in 40 cases after vasoconstriction in the ear but before that in the foot, and in 4 cases before either extremity had vasoconstricted. There was only a low correlation between the ambient temperature at which vasoconstriction occurred and heart rate increased ($r = +0.37$; $P < 0.001$). In general therefore, though not invariably, the metabolic response appeared to follow the vasomotor response.

Usually the onset of shivering coincided with or occurred slightly later than the increase in heart rate. Within individuals the correlation was again low ($r = +0.40$; $P < 0.001$). The low degree of relationship established may stem from the difficulty in fixing accurately the time of increase in heart rate and shivering. At or near the critical temperature transitory fluctuations in heart rate and shivering occurred which probably reflect the balancing of heat production with changing ambient temperature and insulation.

1. Resistance to body cooling

This work extends the previous findings in Blackface sheep by establishing that the resistance of sheep to body cooling can be increased by chronic exposure to moderately sub-critical temperatures as well as by exposure to acute cold. Sheep previously kept at +8°C for two weeks cooled on average at a rate 30% slower than control sheep kept in a thermoneutral environment during the same period.

The responses of sheep to chronic cold exposure were similar in magnitude whether sheep experienced chronic cold alone or chronic cold preceded by acute cold exposure. Thus there appeared to be no additional effect of acute cold exposure. Blackface sheep (Table 3a) showed more acclimatization than the Southdown or Welsh sheep and in particular a clear effect of acute cold exposure alone.

The increased resistance to body cooling shown by Blackface sheep after acute cold exposure resulted from an enhanced ability to maintain normal body temperature coupled with a subsequently decreased rate of body cooling. Both Southdown and Welsh sheep showed only an enhanced ability to maintain body temperature within the normal range. However, this comparison is complicated by the fact that many Blackface sheep showed complete resistance to body cooling on second exposure, within the time period used.

Blackface sheep also showed decreased shivering intensity during acute cold exposure as a result of previous cold experience, while no significant change was observed in the Southdown and Welsh sheep. However, it was considered during discussion of the Blackface data that the large increase in resistance to body cooling shown after acute cold exposure was unlikely to

have resulted solely from the small observed decrease in shivering intensity, and the inferred change in efficiency of heat production. It also seems unlikely that the small change in shivering intensity of the Blackface sheep could account for such a large breed difference in response to acute cold exposure.

Blackface sheep had an initially superior resistance to body cooling than either the Southdown or Welsh sheep. They were therefore exposed to very low temperatures (-20°C) for a longer time during the first cold exposure and could have received a greater stimulus for acclimatization than the other two breeds. But this also seems unlikely since there was no relationship within the Blackface breed between the length of acute cold exposure and the change in resistance to cooling.

It seems probable, therefore, that Blackface sheep simply possessed a much greater capacity to acclimatize than Southdown or Welsh sheep. On this hypothesis, both acute and chronic cold exposure separately produced a degree of acclimatization sufficient to reach this limit. The limit for acclimatization in the Southdown and Welsh sheep would thus be reached in the case of the 8-30 sheep during exposure to +8°C, and in the 30-8 sheep during the first acute cold exposure. Comparison of the amount of acclimatization shown by Blackface sheep to chronic cold exposure alone (chronic cold versus habituation control sheep - Table 13) with that shown as a result of chronic cold exposure after acute cold exposure (HP8 and LP8 sheep - Table 3a) does indicate a limit to acclimatization in the latter sheep which was almost reached as a result of the first acute cold exposure.

Table 29, which summarizes the data for the three breeds, shows the considerable variation which was observed between breeds in initial resistance to body cooling and in ability to acclimatize to cold. Some, though

Table 29. **Comparative resistance to body cooling of Blackface, Southdown and Welsh sheep before and after cold experience**

	Mean rate of decline of rectal temperature (°C/100 min.)					
	n	Blackface	n	Southdown	n	Welsh
a)* Without previous experience of cold	40	0.636 ± 0.058	12	1.105 ± 0.149	12	1.791 ± 0.263
b)+ After experience of acute and chronic moderate cold exposure	20	0.167 ± 0.067	12	0.892 ± 0.201	12	1.220 ± 0.112
c)[2] After experience of chronic cold exposure	8	0.228 ± 0.049	12	0.863 ± 0.130	12	1.084 ± 0.100
(b) as a percentage of (a)		26.3		80.7		68.1
(c) as a percentage of (a)		35.8		78.1		60.5

High and low plane nutrition groups are combined

*Blackface HP8, HP30, LP8 and LP30, and Southdown and Welsh HP and LP 30-8 sheep mean first exposure performance.

+Blackface HP8 and LP8, and Southdown and Welsh HP and LP 30-8 sheep mean second exposure performance.

[2]Blackface HPCC and LPCC, and Southdown and Welsh HP and LP 8-30 sheep mean first exposure performance.

certainly not all, of this variation may have been caused by differences in bodyweight and in the treatments imposed. Because the data were drawn from groups of sheep experiencing slightly different temperature treatments, detailed statistical analyses were not justifiable. Nevertheless it seems clear that the three breeds ranked in the order, Blackface, Southdown, Welsh for initial resistance to body cooling, and that while Southdown and Welsh sheep had similar capacities for acclimatization, Blackface sheep had a much greater capacity. The fact that Southdown sheep had a superior resistance to body cooling than the Welsh was surprising. One may have expected there to be more similarity in initial resistance to body cooling and in ability to acclimatize to cold in the Blackface and Welsh breeds on the assumption that natural selection in the normal habitat of these breeds would have favoured such characteristics. Welsh sheep did tend to show slightly more acclimatization than Southdown sheep, but this was only the case on low plane nutrition. It would not be justifiable at this stage, however, to attempt to project the results from such small numbers to populations of sheep in the field.

An important feature of the data was the considerable variation found between individual sheep of the same sex, and breed and of similar age and weight in their responses to acute cold exposure, despite control of their nutritional and temperature environments throughout the experiments. It is unfortunate that in studies such as these the precise cause of this variation cannot be isolated.

2. Associated physiological responses

The elevated heart rates, rectal, ear, foot and midside temperatures of sheep kept for 2 weeks at +8°C when measured at +30°C before acute cold exposure began can be taken to indicate elevated basal metabolic rates.

These sheep had been in a thermoneutral environment for 18 hours, which would have been sufficient for equilibration of heat production and body temperature, according to the evidence of Joyce and Blaxter (1964a). The inference therefore seems valid. Similar responses were shown by the Blackface sheep after a combination of acute and chronic cold exposure (HP8 and LP8 sheep) and by the smaller groups which had comparable temperature treatment to the Southdown and Welsh sheep (i.e. the high and low plane habituation control and chronic cold sheep). It now seems clear that chronic cold exposure alone was capable of inducing changes in basal metabolism. The elevated heart rates and rectal temperatures of the sheep at +30°C on day 18 confirms the similar trend in the Blackface sheep on day 4, and suggests that basal metabolism in the Southdown and Welsh sheep on day 18 had also been elevated by acute cold exposure two days earlier. Increases in basal metabolism ranging from 20-50% as a result of prolonged cold exposure have been observed in rodents by many workers, cited earlier. Assuming, as before, a linear relationship between heart rate and metabolic rate the Southdown and Welsh sheep apparently showed a 50% increase in basal metabolism similar in magnitude to that shown by the Blackface sheep. Presumably as a result of the inferred increase in basal metabolic rate the critical temperature was lowered. Evidence for this comes from the delayed onset of vasoconstriction. The practical significance of shifting the zone of thermal neutrality to lower ambient temperatures may be to increase the general comfort, mobility and foraging ability of sheep in the field at these temperatures. Energy expenditure, however, would be increased rather than conserved.

Periodic fluctuations in extremity temperature at sub-zero temperatures have been observed previously in sheep (Webster and Blaxter, 1966; Slee, 1966),

in man (Lewis, 1930; Keatinge, 1957) and in various Arctic mammals and birds (Irving and Krog, 1955). Presumably this provides a defence mechanism against tissue injury by freezing, while allowing maximum insulation against heat flow. The tendency shown by all breeds of sheep for cold-induced vasodilatation to increase after prolonged cold exposure would reduce the likelihood of tissue damage by freezing, while at the same time alleviating discomfort and perhaps increasing mobility. This process, as with the change in basal metabolic rate, would involve increased energy expenditure. Increases in vascularity of the ears of rodents have been observed after prolonged cold exposure, leading to increased surface temperatures (Heroux, 1959 and Desmarais and Dugal, 1951) and decreased tissue insulation, (Hart 1957). Moreover reduced tissue damage during cold exposure after previous cold experience has been reported by Blair (1951) and Leblanc (1967).

When kept at subcritical temperatures (+8°C) before and between acute cold exposures sheep of all breeds maintained rectal temperature 0.4°C lower on average than sheep at +30°C. After acclimatization they also allowed rectal temperature to fall during the initial stage of acute cold exposure. These findings are not in line with a strict concept of homeothermy, and suggest that these sheep had voluntarily allowed an adaptive cooling of the body core. Davis (1963) demonstrated similar rectal temperature responses in humans. Those changes took 14 days to develop compared with less than two days in these sheep, but the conditions of exposure were somewhat different. Glaser (1950) demonstrated a similar effect after one day of exposure in humans, although 2 days later rectal temperature had begun to return to normal. These sheep showed no sign of a return to normal after 10 days. Similar but short term effects of ambient temperature on rectal temperatures of sheep have been observed in calorimeters (Webster, 1966) and

in the field in response to diurnal (Eyal, 1963) and annual (Bligh, Ingram, Keynes and Robinson, 1965) temperature rhythms. Possibly by reducing the body core-environment gradient the sheep could maintain body temperature more economically.

These responses can be considered in two ways. They may merely be passive and indicate some degree of thermal instability, in that the animal exerts only rough control of body temperature over moderate ranges of ambient temperature. On the other hand there may have been an active change in response to cold involving a reduction in the temperature threshold for stimulus of receptors controlling heat production. Hammel, Jackson, Stolwijk, Hardy and Strømme (1963) suggested that thermoregulatory responses are proportional to the temperature difference between a 'set point' and the hypothalamic temperature. On their theory, the effect of cold stimuli from peripheral and deep body receptors is to raise the set point relative to hypothalamic temperature thus invoking a thermoregulatory response. Prolonged cold exposure may disturb the relationship between the cold stimulus, the 'set point' and the stimulus for heat production. Either concept may explain the lower rectal temperatures of sheep kept at +8°C between acute cold exposures compared to those of sheep kept at +30°C during the same time. However, during the second acute cold exposure only sheep previously kept at +8°C allowed a fall in body temperature as ambient temperature fell from +30°C to 0°C. This would imply that the second, active type of response had occurred, though the delay in onset of vasoconstriction and consequently reduced peripheral stimulation may, to some extent, have contributed to the response.

Although sheep previously kept at +8°C had comparatively low rectal temperatures during the initial stages of acute cold exposure and at sub-zero

temperatures, this was associated with high extremity temperatures. The extremities therefore appeared to be warmed at the expense of the body core. This is similar to the hypothermic adaptation found in Andean Indians by Elsner (1963). Carlson, Burns, Holmes and Webb (1953) discussed the concept of changes in the distribution of body heat between 'shell' and 'core'; a higher 'shell' heat content coupled with decreased body 'core' heat content being a feature of cold acclimatized animals. Presumably the increased heat loss from the extremities could be supported initially by a loss of body heat from the core at no additional energy cost. This would seem to be of value during short intermittent cold spells. During long term cold exposure, however, energy utilization would have to increase to sustain higher rates of heat loss.

The changes in resistance to body cooling on the one hand, and the changes in basal metabolic rate, distribution of body heat and cold-induced vasodilation on the other, appear to be intrinsically different processes. While changes in all parameters were induced by prolonged moderately sub-critical cold exposure, only the change in resistance to body cooling appeared to be capable of persistence without continued stimulation. This would imply that changes in basal metabolism and the other related parameters are more labile and sensitive to changes in the current environment of the animal. The ambient temperatures at vasoconstriction of the 8-30 sheep on day 2 and the 30-8 sheep on day 16 suggested that the basal metabolism and therefore the critical temperature could be influenced by exposure to both +30°C and +8°C, although sampling effects of small numbers and emotional factors cannot be ruled out. If exposure to +30°C had a positive effect one would have expected the heavier high plane sheep to show a greater reduction in metabolism at +30°C since they would be most sensitive to heat, and low

plane animals being more sensitive to cold to show a greater elevation in metabolism after exposure at +8°C. There was however no evidence to confirm this.

3. The mechanism of acclimatization

The precise mechanism of the improvement in resistance to body cooling as a result of chronic or acute cold exposure is not clear. Although prolonged cold exposure consistently caused increases in skinfold thickness, this change could not be related to changes in skin temperature, which would have implied altered insulation. The factors involved in these short-term increases in skinfold thickness are not clear. Baker (1960) found an increase in the water content of the skin of rats after prolonged cold exposure but did not measure skinfold thickness. Wodzicka-Tomaszewska, (1960a) on the other hand, showed only an initial transitory increase in the water content of sheep skin. She found no evidence to suggest that changes in fat content or in vasomotor tone were implicated but concluded that some change in skin histology had probably occurred. Very recent work, not reported in this thesis, has suggested that increased water content could be responsible for the increase in skinfold thickness even after 2 weeks exposure to cold. Comparison of the thermal conductivities of water, the dermis and the epidermis (Tregear, 1966) leads one to the conclusion that the insulation of the skin may in fact have decreased. In view of this and the generally increased skin temperatures after acclimatization the change in resistance to cooling would not appear to have resulted from increased tissue insulation.

Although Blackface sheep kept at +8°C between acute cold exposures did have higher heart rates at sub-zero temperatures during second cold exposure and a greatly increased resistance to cooling, there was no consistent

evidence from the heart rates of other groups of sheep to suggest that maximum metabolic capacity was increased. However a high correlation between metabolic rate and heart rate has only been established over a small range of heat production (Blaxter, 1948; Webster, 1967). Extrapolation of the heat losses of the two sheep of Graham et al. (1959) to an ambient temperature of -20°C showed that for body temperature to be maintained heat production would have to increase to six times the basal level. Some of the present sheep with a similar amount of fleece insulation were able to maintain body temperature at -20°C in a 4 m.p.h. wind and despite convulsive shivering, which suggests a considerably greater than six-fold increase in heat production. Hutchinson (1965-66) has reported summit metabolic rates eight times higher than the basal level. Heart rates of the present sheep showed only a threefold increase. There seems no doubt that the relationship between heart rate and metabolic rate breaks down at high levels of metabolism. In this context Wyndham, Strydom, Maritz, Morrison, Peter and Potgeiter (1960) found a linear relationship in men between heart rate and metabolic rate up to a maximum heart rate of 180 beats/min. Thereafter oxygen consumption increased with little or no change in heart rate. In the present sheep a similar limit to heart rate may have existed. However the fact that sheep with an initially poor resistance to cooling were able to maintain body temperature at lower ambient temperatures after acclimatization, while the survival time at -20°C of the initially more resistant sheep was increased, suggests that in some cases the level of summit metabolism was raised, while in others the capacity to maintain summit metabolic rates was increased. This view is supported by the evidence from work with rodents, in which increased summit metabolic rates or the capacity to maintain these are the most consistent features of acclimatization.

The possibility discussed previously, that a change in the efficiency of heat production may have contributed to the response in Blackface sheep cannot be excluded.

4. Influence of nutrition and bodyweight

In these experiments acclimatization occurred although both high and low plane rations were fixed during the treatment period. High plane sheep had greater initial resistance to cooling than low plane sheep, though generally showed only similar amounts of acclimatization. But the data from the low plane Welsh sheep, and from the subsidiary Blackface sheep subjected to the same temperature treatment as the Southdown and Welsh group (i.e. the HPHC and LPHC and HPCC and LPCC sheep) did suggest that low plane sheep might show more acclimatization than high plane sheep after chronic moderate cold treatment. Moreover there was a tendency for the Blackface LP8 sheep to show either considerable acclimatization or none at all. This raises the question of the optimum cold dosage required for acclimatization. Possibly high plane sheep with greater insulation and basal heat production require a relatively large dosage of cold to produce maximum acclimatization, whereas low plane animals require a smaller cold dosage, which may easily be exceeded with a resultant induction of debility. However, it seems that this hypothesis regarding the size of stimulus and the response may not be applicable to all breeds since low plane Southdown sheep showed comparatively little acclimatization. The relationships between the size of the stimulus, the condition of the individual animal and the response deserve more detailed investigation.

Blair (1951) and Hart (1957) have suggested that acclimatization increases the ability to utilize body reserves and so causes weight loss. Most of the present sheep lost weight while in the cold, but no significant relationship

was found between weight change and degree of acclimatization. Nevertheless, many sheep showed large improvements in performance despite considerable losses in bodyweight.

5. Significance of the findings

The question then arises as to the relevance of these changes to the performance of sheep in the field. It can be argued that sheep in winter are unlikely to experience conditions so severe as the acute cold exposures used in this experiment, since they would normally be in full fleece when the most inclement weather prevails. However, severe conditions will be encountered by hill sheep, resulting from prolonged periods of food shortage coupled with low temperatures, and wind and rain which will tend to reduce the insulation of the fleece. Moreover, during bad weather shearing does impose a considerable cold stress on the animal and losses are known to occur (Hutchinson, Bennett and Wodzicka-Tomaszewska, 1960). Under such conditions the capacity of sheep to mobilize and utilize body reserves may be influenced by the ability to acclimatize. The applicability of these findings in shorn sheep to the fleeced sheep has, however, yet to be tested.

The significance of acclimatization is obvious in experiments concerning the physiological responses of sheep to cold, particularly when it is important to assess genetic and environmental sources of variation. The previous thermal history of the animals may then be highly relevant. Moreover, in experiments where the same sheep are subjected to repeated cold exposures then the later results may be influenced by previous treatment. Ultimately the considerable individual variation which has been found both in initial cold resistance and in the ability to increase resistance may open up new possibilities for genetic selection on either or both of these criteria. However, much further work will be required to establish the heritability of cold resistance and its relevance as a character to performance in the field.

SUMMARY

This work has shown that considerable variation may exist in shorn sheep, both within and between breeds, in the ability to maintain rectal temperature under acute sub-zero cold exposure (-20°C, 4 m.p.h. wind). The mean rates of decline of rectal temperature in Blackface, Southdown and Welsh sheep were 0.636, 1.105 and 1.791°C/100 min. exposure respectively. Differences in bodyweight, although quite large, could not account for all the variation observed between breeds. Within breed coefficients of variation were large, ranging from 25% to 66%. High plane sheep had greater cold resistance than low plane but there was no evidence for breed x nutrition interactions. Individual repeatability of performance was quite high, ranging from +0.35 to +0.96 within groups.

The work has shown that low temperature exposure can induce rapid and significant physiological changes in shorn sheep. These include changes in resistance to body cooling under acute cold exposure, defined as acclimatization, changes in basal metabolic rate and changes in the distribution of body heat. Acclimatization was clearly induced in all breeds of sheep by 2 weeks exposure to moderate cold (+8°C). Acute cold exposure (usually sufficient to lower body temperature by several degrees) also clearly caused acclimatization in Blackface sheep. Blackface sheep had a much greater capacity for acclimatization than either Southdown or Welsh sheep. The mean rates of decline of rectal temperature in the three breeds were 74%, 19% and 32% slower respectively after acclimatization. In general both high and low plane sheep showed similar amounts of acclimatization but there was evidence, though inconclusive, for possible breed x nutritional interactions in ability to acclimatize.

It was concluded from indirect evidence and by analogy with previous work on rodents that acclimatization probably resulted from an enhanced capacity of the sheep to maintain increased rates of metabolism under cold exposure. A slight change in the efficiency of heat production involving a reduction in shivering thermogenesis may have contributed to the response in Blackface sheep.

Prolonged moderate cold exposure caused an elevation in rectal and skin temperatures and in heart rate when subsequently measured at a thermo-neutral temperature. Rectal temperatures were, on average, 0.15°C higher, ear and foot temperatures were 3.2 and 2.5°C higher respectively, and heart rates increased by 40-50% after moderate cold exposure. This implied a considerable increase in the basal metabolic rate and it resulted in a lowering of the critical temperature, as shown by delayed vasomotor responses under subsequent cold exposure. Vasoconstriction occurred, on average, 4°C and 7°C later in the ears and feet respectively after prolonged moderate cold exposure. Acute cold exposure also appeared to cause an increase in basal metabolic rate as judged by heart rates measured two days later.

Sheep kept at moderately sub-critical temperatures for long periods of time allowed, on average, a reduction in body temperature of 0.4°C. This effect was also shown during initial stages of subsequent acute cold exposures. On subsequent sub-zero cold exposure these sheep also showed increased cold-induced vasodilatation of the ears, an effect likely to reduce tissue damage.

The increase in resistance to body cooling and the associated physiological responses appeared to have slightly different properties. While increased resistance to body cooling and the associated responses were both induced by prolonged moderate cold exposure, only the increased

resistance to body cooling was able to persist without continuous stimulation.

A high correlation was found between shivering intensity and heart rate under cold exposure.

Prolonged cold exposure caused a 20-30% increase in skinfold thickness, but this could not be related to the change in resistance to body cooling.

It was stressed in discussion that the applicability of these findings in shorn sheep to fleeced sheep, and the relevance of resistance to cooling as a character related to performance in the field, have yet to be tested. Nevertheless, it was suggested that these changes induced by exposure to cold may be of considerable importance to sheep in the field especially after shearing and of fundamental importance to physiologists and geneticists in studies of the cold resistance of sheep.

PART 3 - ACCLIMATIZATION OF LAMBS TO COLD

In view of the results from adult sheep, it was considered that the effects of acclimatization might be very important in lambs with no previous cold experience. Moreover, it is at this stage of life that any ability to acclimatize to cold would most influence survival. This section describes a small experiment designed to show whether new born lambs are capable of acclimatization to cold.

MATERIALS AND METHODS

Eight Scottish Blackface in-lamb ewes were brought into individual pens inside the climate chambers one week before they were due to lamb. All were fed 2,000 gm/head/day of the standard pelleted ration. Four were shorn and kept at +25°C - the estimated thermoneutral temperature for young lambs (Alexander and Williams, 1962). Ambient temperature for the other four (in full fleece) was maintained between 0°C and +2°C. Five lambs (4 singles and 1 pair of twins) were born into each environment and maintained there for 2 weeks before receiving an acute cold exposure. They are subsequently referred to as the L25 and L0 lambs respectively.

Rectal temperature was measured 2 hrs. after birth and at intervals up to 2 weeks of age at the respective treatment temperatures. On the morning of acute cold exposure the lambs were removed from the ewe at 06.30 hrs., closely shorn with 'Oster' small animal clippers and put in a climate chamber at +30°C. The lambs were yoked by the neck in a standing position, and supported under the belly by a loose string mesh cradle. Equipment similar to that described for adult sheep was used to record left ear, foot and midside temperatures. Rectal temperature was measured by a thermocouple

inserted 5 cm. The onset of shivering was assessed by visual observation. All equipment was fixed by 08.30 hrs. During cold exposure, commencing at 10.30 hrs., ambient temperature was lowered from +30°C to +10°C at a rate of 1°C/5 min., and maintained at +10°C for 45 min. until 12.45 hrs. A 4 m.p.h. wind was then introduced and ambient temperature lowered rapidly to -15°C. Lambs were removed from the chamber when rectal temperature had fallen to 36°C.

The L25 twin lambs and a single LO lamb were found to have been sired by a Welsh and not, as intended, by a Blackface ram. There was, however, no evidence to warrant their exclusion from the results.

RESULTS AND DISCUSSION

Birthweights of both groups of lambs were similar, and each group maintained a similar mean rate of growth in the two weeks before acute cold exposure (Table 30). The L25 lambs showed no signs of heat stress, though occasionally after handling they were observed to pant.

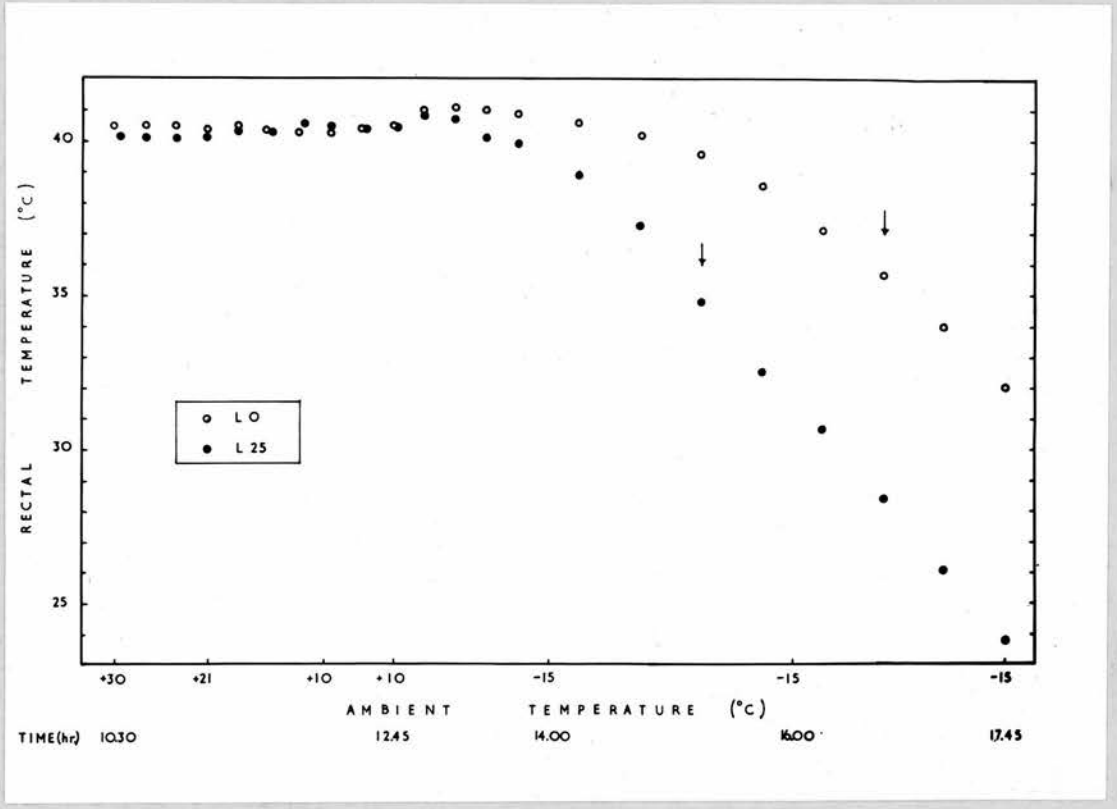
Rectal temperatures of L0 lambs were 0.7°C higher, on average, than those of the L25 lambs 2 hrs. after birth (Table 30). Within 2 days, however, the situation was reversed. Rectal temperature of L0 lambs had fallen slightly while those of the L25 lambs had increased considerably (Table 30). Throughout the remaining 2 weeks rectal temperatures of L25 lambs were slightly, though not significantly higher than those of L0 lambs. This suggests that the L0 lambs had initially shown a rapid increase in heat production in response to the low environmental temperature and the need to evaporate moisture from the coat. Those born at +25°C probably had no need to increase heat production appreciably, since much of the heat required to dry the coat would be provided by the environment. Alexander and McCance (1958) showed that rectal temperatures of lambs fell initially at birth, then rose to a peak within a few hours and subsequently declined gradually. The present data suggest that this rise in rectal temperature may, to some extent, be related to the environmental stimulus for heat production.

Fig. 19 shows the changes in mean rectal, midside, ear and foot temperatures of the two groups of lambs during acute cold exposure. Rectal, midside, ear and foot temperatures of L0 lambs were slightly, though not significantly, higher than those of L25 lambs at +30°C before exposure. As ambient temperature fell between +30°C and +10°C rectal temperatures of lambs previously kept at +25°C showed a gradual increase, while those of lambs kept at 0°C showed little change. On the commencement of rapid environmental

Table 30. Bodyweight and Rectal Temperature

Treatment group	bodyweight (kgm.)		rectal temperature (°C)	
	At birth	At 2 weeks	At birth	At 2 days
L0	4.4 ± 0.14	7.2 ± 0.42	40.4 ± 0.16	39.9 ± 0.11
L25	4.0 ± 0.37	7.1 ± 0.66	39.7 ± 0.17	40.8 ± 0.11
Significance of the difference between L0 and L25 lambs (P)	N.S.	N.S.	<0.05	<0.05

(a)



(b)

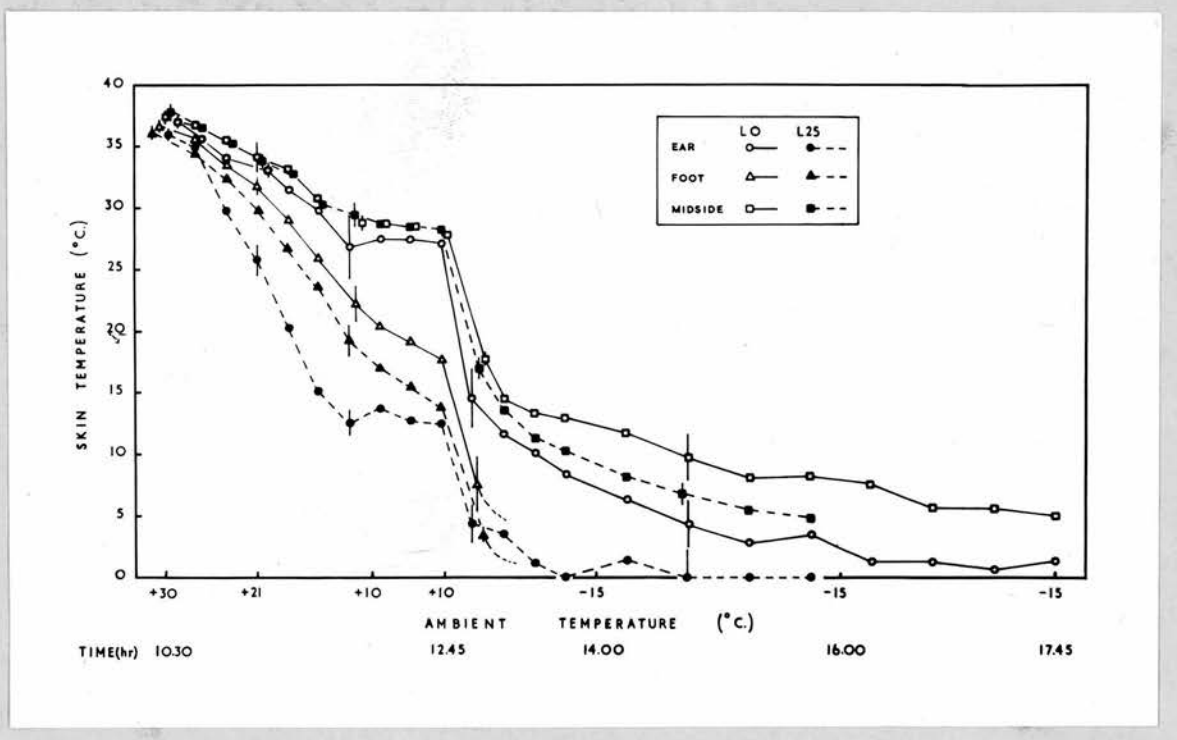


Fig. 19 The changes in (a) mean rectal and (b) mean ear, foot and midside temperature in the LO and L25 groups (5 lambs per group) during acute cold exposure.

Ambient temperature was lowered progressively according to the time scale shown. Arrows indicate the point from which the mean is comprised of extrapolated data from more than two individuals.

cooling both, but especially the latter, showed an increase in rectal temperature, and subsequently the LO lambs showed a slower rate of body cooling than the L25 lambs. The mean rates of body cooling were 1.998 ± 0.167 and 2.800 ± 0.314°C/100 min. for LO lambs and L25 respectively, measured from 12.45 hrs. when rapid cooling was introduced. The difference between groups was significant only at the 10% level.

The changes in ear and foot temperature followed similar patterns to those of adult sheep. Vasoconstriction was delayed in LO lambs (Table 31 and Fig. 19) resulting in higher ear and foot temperatures during the initial stages of cold exposure, though the differences between groups were generally not significant. Similarly, shivering tended to be delayed until lower ambient temperatures in the LO compared to the L25 lambs (Table 31) but the difference between groups was not significant. These changes, and the higher skin and rectal temperatures of the LO lambs at +30°C, suggests that, as in adult sheep, basal metabolic rates may have increased as a result of prolonged cold exposure.

At sub-zero temperatures, ear temperatures of LO lambs were slightly, though again not significantly, higher than those of the L25 lambs. Foot thermocouples invariably came off as the lambs began to struggle. Three of the five L25 lambs, however, showed a slight swelling and tenderness of the hocks after acute cold exposure, which was not observed in any of the LO lambs. Although no direct evidence was obtained to suggest that cold-induced vasodilatation occurred more frequently in the LO lambs, due to the difficulty in keeping thermocouples on the feet of lambs, it seems probable that some physiological change may have occurred which reduced cold trauma. Blair (1951) and Leblanc (1967) have shown that cold-acclimatized rats suffered less frostbite than non-acclimatized rats on cold exposure.

Table 31. Vasoconstriction and Shivering

Treatment group	Mean ambient temperature and ear and foot skin temperature at vasoconstriction				Ambient temperature at onset of shivering (°C)
	Ear		Foot		
	Ambient (°C) Temperature	Ear (°C) Temperature	Ambient Temperature	Foot Temperature	
L0	15.6 ± 3.04	31.7 ± 0.84	22.2 ± 1.38	32.9 ± 1.08	16.4 ± 2.29
L25	27.6 ± 0.75	34.5 ± 0.72	27.8 ± 0.37	34.9 ± 0.27	21.8 ± 1.44
Significance of difference between L0 and L25 (P)	<0.01	<0.05	<0.01	N.S.	N.S.

In conclusion, although the differences between groups rarely attained statistical significance due partly to the small numbers involved, these results suggest that lambs, like adult sheep, possess the ability to acclimatize to cold. The degree of acclimatization shown as a result of prolonged low temperature exposure was of a similar magnitude (30%) to that shown by adult sheep. It seems probable that this was the result of an increase in the summit metabolic capabilities of the lambs since, if anything, heat losses were increased from the extremities. This conclusion is supported by reported increases in the summit metabolic rates of shorn lambs after prolonged exposure to 35°F (Alexander 1964-65). The higher rectal, ear and foot temperatures of lambs previously kept at 0°C when measured in a thermoneutral environment and their subsequently delayed vasomotor and shivering responses, suggest that basal metabolic rates were also elevated as a result of cold exposure. However, as with much of the work on rodents, it is clear that some of these changes may have been a consequence of increased food intake.

SECTION B

SOME COMPARATIVE RESPONSES TO COLD EXPOSURE OF SCOTTISH BLACKFACE, SOUTHDOWN AND WELSH MOUNTAIN SHEEP IN FULL FLEECE

INTRODUCTION

The efficiency with which an animal survives in a cold environment depends upon the extent to which it has to increase heat production above the basal level in order to maintain body temperature. It is assumed that vasomotor responses in the extremities generally occur close to or just prior to the metabolic response in sheep (Blaxter et al., 1959) and in pigs (Mount, 1964a). It was therefore considered that the onset of vasoconstriction may provide some estimate of the critical temperatures of sheep and give some measure, therefore, of their sensitivity to cold.

Slee (1964 and 1968) has observed variation between breeds in vasomotor responses which were probably related to differences in fleece type and morphology. Moreover, variation in insulation is associated with fleece type (Alexander, 1958; Blaxter, Clapperton and Wainman, 1966) and length (Armstrong et al., 1960). Doney (1963) has related differences in bodyweight loss over winter to fleece depth, fleece weight and fibre density.

This section compares the cold-induced vasomotor responses of three breeds of sheep. An attempt was made to relate these responses to variation in bodyweight, nutrition, fleece length, wool weight/unit area and skinfold thickness.

MATERIALS AND METHODS

The 48 Scottish Blackface, 30 Southdown and 30 Welsh Mountain sheep described in Section A were used. Experiments were carried out approximately three weeks after allocation to nutritional treatments, before the main acclimatization experiments began. All sheep had by this time been indoors on controlled feeding for 5-6 weeks.

The day prior to treatment sheep were brought into a climate chamber by 17.00 hrs. and maintained there overnight at a thermoneutral ambient temperature. This was assessed for these sheep on the basis of their average fleece length by reference to the data of Armstrong et al. (1960). For the Blackface sheep in 1965, temperatures of +8°C and +10°C were used for the high and low plane sheep respectively, but in 1966 these were modified for the high and low plane Southdown and Welsh sheep to +13°C and +15°C respectively. Next morning at 08.00 hrs. the sheep were yoked and equipment for recording rectal, left ear, foot and midside temperatures, heart rates and respiration rates was fitted. Small areas of skin were clipped for the attachment of thermocouples. The equipment was identical to that described previously. The sheep then remained undisturbed for at least one hour before a slow fall in ambient temperature (1°C/30 min.) was introduced at 10.00 hrs. This continued until complete vasoconstriction was shown in the ear and foot or until the ambient temperature reached -5°C (Blackface) or -2°C (Southdown and Welsh), whichever occurred sooner. These lower limits were set to minimise any effects that this cold exposure might have on the subsequent acclimatization experiments. Rectal, ear, foot and midside temperatures were recorded every 5 min., and heart rate and respiration rate at half-hourly intervals immediately preceding the

changes in ambient temperature.

All sheep were fed maintenance rations at 07.00 hrs. on the morning of the test and the amount consumed by 08.00 hrs. was recorded. Bodyweight was measured 8 hrs. after feeding on the day prior to treatment. At the same time fleece depth was assessed by probe at nine sites. These were:- along the dorsal line - at the withers, midback and sacral regions; laterally - on the right shoulder, right midside and right britch; and ventrally - on the chest, belly and udder. In the computation of mean fleece length the lateral measurements were counted twice. A sample of wool, from an area delineated by 10 sq.cm calipers on the right midside just posterior to the last rib, was also taken at this time. All wool samples were conditioned and weighed together. Skinfold thickness, the mean of two skin pinches taken at right angles to each other on the same site, was measured by Harpenden spring calipers.

Quartets of sheep on high and low plane nutrition were treated on alternate days. In 1966 each quartet contained two Southdown and two Welsh sheep.

Forty Blackface sheep and all the Southdown and Welsh sheep, equal numbers on high and low plane nutrition, were treated in this way. The remaining Blackface, 6 high and 2 low plane, served as controls to assess any diurnal changes in the measured characters. They received exactly the same treatment except that ambient temperature remained constant. Three sheep from each of the Southdown and Welsh groups (12 in all) also served as controls one week prior to temperature treatment.

1. Bodyweight, fleece length, wool weight/unit area, skinfold thickness and food consumption

Table 32 gives the mean bodyweight, fleece length and wool weight/unit area and skinfold thickness measured the day before exposure, and mean food consumption on the day of the test. Of these parameters only bodyweight was influenced by the nutritional treatments established three weeks prior to test. Within breeds the differences in bodyweight between high and low plane nutrition sheep were highly significant ($P < 0.01 - 0.001$) in all cases. The breeds ranked in the order Blackface, Welsh and Southdown for length of fleece and wool weight/unit area, the differences between breeds being highly significant ($P < 0.001$) in all cases. However for skinfold thickness the situation was exactly the reverse. Southdown sheep had slightly though not significantly greater skinfold thickness than Welsh sheep, but both had greater skinfold thickness than Blackface sheep ($P < 0.01$ and < 0.05 respectively, combining nutritional groups). Although this suggests a tendency for sheep with longer and heavier fleeces to have a smaller skinfold thickness, there was no such relationship within breeds. In general, low plane sheep consumed more of the maintenance ration before test than did high plane sheep, and Blackface sheep tended to refuse a greater proportion of their ration than sheep of the other two breeds.

2. Rectal temperature

Rectal temperatures of the three breeds of sheep - Fig. 20, were similar throughout exposure, and invariably showed a gradual fall. Control sheep which were kept in the chamber at a constant temperature showed a

Table 32. Mean bodyweight, fleece length, wool weight/unit area, skinfold thickness and food intake of Blackface, Southdown and Welsh sheep in full fleece

Parameter	Breed	Blackface		Southdown		Welsh	
	Nutrition	High	Low	High	Low	High	Low
	n	20	20	15	15	15	15
Bodyweight (kg.)		29.9 ± 0.66	27.0 ± 0.56	27.6 ± 0.72	24.4 ± 0.58	21.7 ± 0.38	18.5 ± 0.27
Fleece length (cm.)		9.4 ± 0.21	9.4 ± 0.25	4.5 ± 0.12	4.3 ± 0.14	6.1 ± 0.15	6.0 ± 0.15
Fleece weight/10cm^2 (gm.)		2.37 ± 0.127	2.43 ± 0.141	1.41 ± 0.047	1.43 ± 0.043	1.59 ± 0.091	1.73 ± 0.043
Skinfold thickness (mm.)		3.4 ± 0.09	3.2 ± 0.11	3.8 ± 0.13	3.6 ± 0.20	3.6 ± 0.12	3.5 ± 0.16
Food intake (gm.)		325 ± 53.4	518 ± 35.4	498 ± 53.9	555 ± 19.9	352 ± 43.8	453 ± 7.5

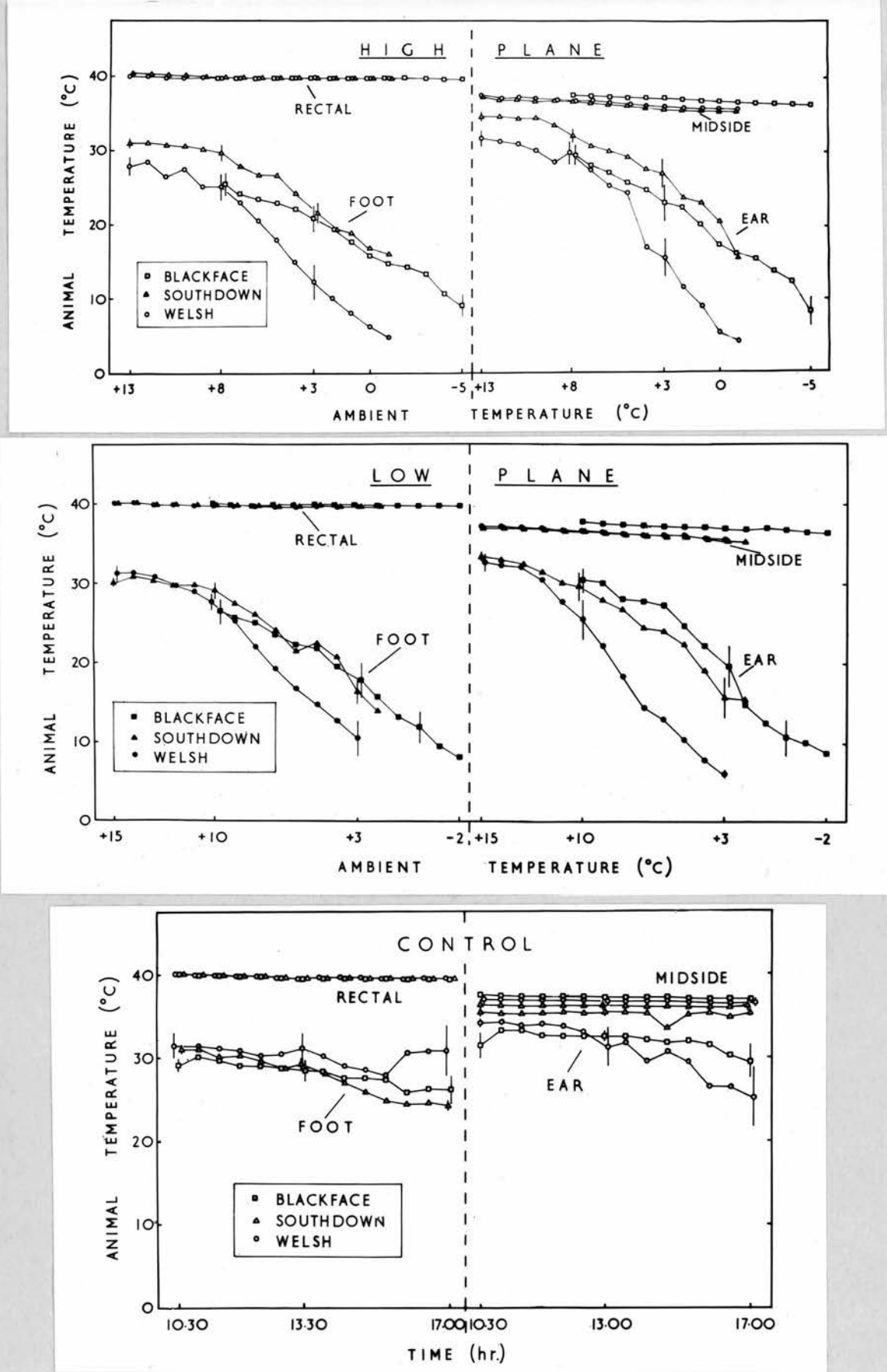


Fig. 20. The changes in mean rectal, midside, foot and ear temperatures of high and low plane sheep during cold exposure, and of control sheep kept in the climate chambers during the same time period at a constant ambient temperature.

similar fall in rectal temperature during the same time period. This may represent a gradual decay of emotional disturbances caused during the fixing of equipment and possibly some diurnal variation. Occasional increases in rectal temperature were observed, often in association with vasomotor responses, probably reflecting a reduction in the amount of blood flowing through the cold extremities.

3. Midside temperature

Midside temperatures of all groups of sheep showed similar changes during cold exposure - Fig. 20. Midsides cooled at rates which varied from 0.03 - 0.23°C/°C fall in ambient temperature, the overall mean rate of fall being 0.12 ± 0.045°C/°C fall in ambient temperature. Midsides of control sheep cooled only slightly during the same time. There was no relationship between fleece length or wool weight/unit area and the rate of cooling of the midside. However, Blackface sheep had higher midside temperatures throughout exposure than either Southdown or Welsh sheep at any environmental temperature. Thermal circulation indices (Table 33) show clearly that the ratio of external to internal insulation was greater in the Blackfaces than in either of the other two breeds ($P < 0.001$ at +3°C, nutritional groups combined). Theoretically this could be either the result of greater fleece insulation, lower tissue insulation, or a combination of the two. Blackface sheep had greater fleece length and wool weight/unit area, and smaller skinfold thickness than Southdown or Welsh sheep. But no significant relationship could be established within breeds, between thermal circulation indices and these parameters. When subsequently shorn (Section A) midside thermal circulation indices in the three breeds were never significantly different. This suggests that in the present results the Blackface sheep may have had greater fleece insulation.

Table 33. Mean thermal circulation indices on the midsides of sheep during cold exposure

Ambient Temperature (°C)

Treatment	Group	n	+15	+13	+10	+8	+3	0	-5
Blackface	High	20				12.6 ± 0.78	13.4 ± 1.00		11.36 ± 0.93
	Low	20			13.4 ± 0.95		12.3 ± 0.86	12.30 ± 0.69	
Southdown	High	15		8.6 ± 0.97		9.4 ± 1.07	8.7 ± 0.30		
	Low	15	8.2 ± 0.83		9.5 ± 1.14		9.0 ± 0.89		
Welsh	High	15		9.5 ± 0.54		9.8 ± 0.55	9.2 ± 0.57		
	Low	15	9.2 ± 0.80		10.4 ± 1.01		9.7 ± 0.94		

4. Ear and foot temperatures

The changes in mean ear and foot temperatures are shown in Fig. 20. The ears and feet of a few sheep were showing slight vasoconstriction at the commencement of exposure. This was presumed to be due to emotional disturbance, since in the majority of cases it was relaxed before any change in ambient temperature. As the environment cooled, vasomotor responses occurred in the ears and feet of most sheep, resulting in rapid falls in skin temperature. Table 34 shows the mean ambient and skin temperatures at which vasoconstriction occurred. It was apparent that some of the smaller sheep of all breeds were close to or slightly below their critical temperatures at the commencement of exposure, as judged by their degree of vasoconstriction. For these sheep vasoconstriction was judged to have occurred at the starting temperature provided that vasoconstriction was maintained and the other extremity vasoconstricted at a similar ambient temperature. One Southdown sheep did not show vasoconstriction of either extremity, another showed vasoconstriction only in the foot, while three Blackface sheep showed vasoconstriction only in the foot. For these sheep, vasoconstriction was scored at the lowest ambient temperature used ($-5^{\circ}C$ for Blackface sheep, $-2^{\circ}C$ for Southdown and Welsh). These methods were justified on the grounds that differences between treatment groups would thus, if anything, be reduced. There was no consistent difference between extremities in the ambient temperature at which vasoconstriction occurred. This contrasted with the situation in the same sheep after shearing, where vasoconstriction of the foot invariably occurred at an ambient temperature several degrees lower than that in the ear (Section A). There was, in the present experiment, a correlation within individuals between the ambient temperature at which vasoconstriction occurred in the ears and feet

Table 34. Mean ambient temperature (°C) and mean skin temperature (°C) at onset of vasoconstriction in the ears and feet

	Blackface n = 20		Southdown n = 15		Welsh n = 15	
	Ambient Temperature	*Skin Temperature	Ambient Temperature	*Skin Temperature	Ambient Temperature	*Skin Temperature
			EARS			
High Plane	0.4 ± 0.95	28.1 ± 0.98	1.8 ± 0.83	30.8 ± 0.71	5.7 ± 0.89	30.4 ± 0.64
Low Plane	1.8 ± 0.80	30.1 ± 0.87	5.5 ± 1.09	30.9 ± 0.56	9.1 ± 0.65	30.8 ± 0.54
			FEET			
High Plane	2.3 ± 0.96	25.6 ± 0.58	2.5 ± 0.84	26.5 ± 0.89	6.7 ± 0.89	27.2 ± 0.96
Low Plane	3.3 ± 1.01	25.1 ± 0.79	6.9 ± 0.87	28.4 ± 0.95	8.2 ± 0.82	27.6 ± 0.78

* Skin temperature was that recorded immediately prior to vasoconstriction

($r = +0.61$; $P < 0.001$). Vasoconstriction of both the ears and feet occurred later in high than in low plane sheep, Table 34. Within breed groups the differences were not always statistically significant, but when breeds were combined the difference was highly significant ($P < 0.01$) in both extremities. However for vasoconstriction in both ears and feet the breeds could be ranked Welsh, Southdown and Blackface in order of response. The smallest difference between treatment means for significance at the 5% level was 3.2°C and 3.8°C for the ears and feet respectively. In general the differences between the Welsh and the other two breeds, especially the Blackface, were statistically significant, but those between Blackface and Southdown sheep were not.

Actual ear temperatures were, on average, 3.4°C ($P < 0.001$) higher than foot temperatures at vasoconstriction though ear and foot skin temperatures of the three breeds were generally similar. There were large differences in the amount of fall of extremity temperature after vasoconstriction ranging from 2.0 to 19.0°C in the ears and from 1.6 to 6.3°C in the feet during the ten minutes immediately after vasoconstriction. However, this was almost entirely related to the temperature gradient which obtained between the environment and the skin immediately prior to vasoconstriction (Table 35). Feet and ears cooled at similar rates in the different breeds though the rate of cooling of ears was twice as great as that of the feet ($P < 0.001$).

The increase in heat production on cold exposure, which determines the critical temperature, is generally accepted to occur when the animal has reached its maximum capacity for heat conservation. It was considered that the best estimate for the critical temperature of these sheep would be the ambient temperature obtaining when both extremities had vasoconstricted.

Table 35. Mean rates of fall of ear and foot temperatures in the 10 min. immediately following vasoconstriction, expressed per unit of temperature gradient between the extremity and the environment

	Blackface n = 20		Southdown n = 15		Welsh n = 15	
	Ear	Foot	Ear	Foot	Ear	Foot
High Plane	0.41 ± 0.028	0.14 ± 0.012	0.40 ± 0.043	0.18 ± 0.027	0.47 ± 0.040	0.21 ± 0.021
Low Plane	0.46 ± 0.027	0.19 ± 0.029	0.43 ± 0.047	0.17 ± 0.067	0.43 ± 0.042	0.18 ± 0.017

Critical temperatures were therefore calculated in this way, (Table 36a). It was realised that some errors would be introduced, as no account could be taken of the behaviour of the right ear and foot. However these may be small, since Slee (1968) has found high correlations within individuals between the ambient temperatures at which right and left ear and right and left foot vasoconstrict. In an attempt to account for variation in the estimated critical temperature by variation in fleece length, wool weight/unit area, bodyweight, skinfold thickness and food consumed on the day of the test, partial regression coefficients were calculated. Within the separate breed x nutrition groups residual degrees of freedom were small after removal of those due to regression. The partial regression coefficients given in Table 37 were therefore derived after combining the data by fitting constants for the breeds and for plane of nutrition, and are based on the deviation of each character from the inter-breed mean. These show that variation in fleece length and in the amount of food consumed on the day of the test had significant influences on the estimated critical temperature, while the effect of bodyweight was not quite significant.

The estimated mean critical temperatures of the three breeds on high and low plane nutrition at the inter-breed means of the measured characters were then determined (Table 36b). Some caution should be exercised in the interpretation of these corrected values in view of the low significance levels of some coefficients. However, the variation between breeds was significant, Table 38a, but the ranking was changed. Southdown sheep now had a much lower critical temperature than either of the other two breeds while Welsh sheep were intermediate. The comparatively low critical temperature of the Southdown sheep may possibly be explained by their fleece morphology. These sheep, although possessing a generally shorter fleece, had more wool cover on

Table 36.

Critical Temperatures

		a) Estimated critical temperature (°C)		b) Estimated critical temperature after correction to standard fleece length, wool weight/unit area, bodyweight, skinfold thickness and food consumption on test day	
Breed	n	High Plane	Low Plane	High Plane	Low Plane
Blackface	20	0.1 ± 0.94	1.5 ± 0.79	5.0	6.8
Southdown	15	1.6 ± 0.62	4.8 ± 0.62	-1.3	0.5
Welsh	15	5.3 ± 0.99	7.6 ± 0.80	2.3	4.1

Table 37.

Partial coefficients for the regression of estimated critical temperature on fleece weight, fleece length, bodyweight, skinfold thickness and food consumption after fitting constants for breeds and plane of nutrition

Parameter	Partial regression coefficient b.	S.E.	P
Fleece weight	-0.010	0.009	N.S.
Fleece length	-0.015	0.005	<0.01
Bodyweight	-0.029	0.016	N.S.
Skinfold thickness	+0.018	0.065	N.S.
Food consumption on test day	-0.005	0.002	<0.05

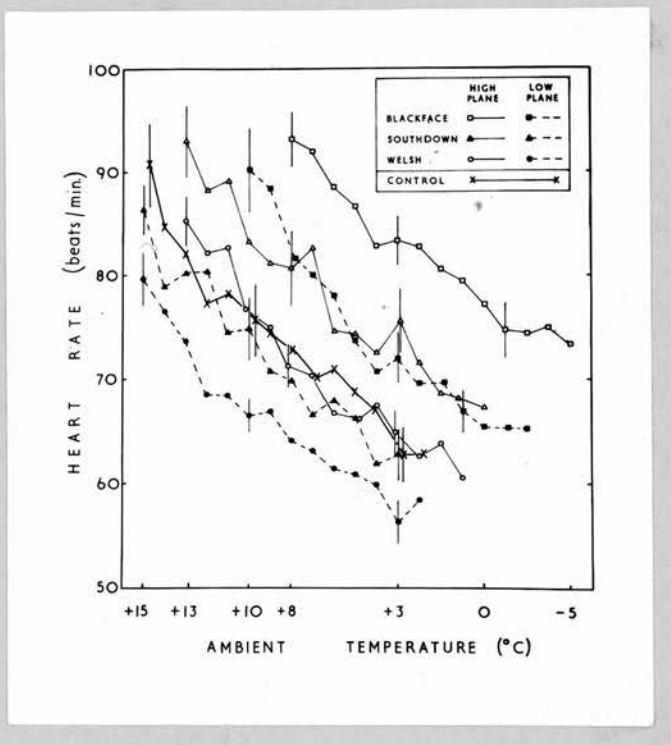
Table 38. Analysis of variance for critical temperature, after fitting constants for breeds and for regression on fleece weight, fleece length, bodyweight, skinfold thickness and food consumption

Source of variation	df.	(a) S.S.	(a) M.S.	(a) F	(a) P	(b) substituting log. fleece length and bodyweight$^{0.7}$ S.S.	(b) M.S.	(b) F	(b) P
Between breeds	2	101.18	50.59	3.47	<0.05	108.10	54.05	4.79	<0.02
Other effects including regression and plane of nutrition	6	833.50	138.92	9.54	<0.001	831.05	138.51	12.26	<0.001
Residual	91	1032.52	14.56			1028.05	11.29		
Total	99	1967.20				1967.20			

the ears and feet than the hill breeds. Presumably therefore their extremities were better insulated. The variation between Welsh and Blackface sheep is more difficult to explain. Armstrong et al. (1960) demonstrated a curvilinear relationship between fleece length and insulation, such that the change in insulation per unit length was greatest in short fleeces. Thus it may well have been that the regression introduced an unfair bias against the longer-fleeced Blackface sheep. Similarly the use of bodyweight, rather than surface area which is more closely related to heat loss, may also have contributed to a bias against the heavier Blackface sheep. Regression coefficients were therefore recalculated introducing the logarithm of fleece length and bodyweight to the power of 0.7. Although slightly more of the total variation in critical temperature was accounted for in this way (Table 38b), the adjusted group mean critical temperatures were not significantly changed.

5. Heart rates

Fig. 21 shows that changes in heart rate were similar in the treated (cold exposed) and in the control sheep (at a thermoneutral temperature), and were related to the time after fixing of recording equipment. High plane sheep generally had higher heart rates than low plane sheep ($P < 0.001$) while heart rates of Welsh sheep were lower ($P < 0.001$) than those of either the other two breeds. Presumably since critical temperatures were generally only just attained the metabolic response was insufficient to produce easily detectable changes in heart rate. However at the end of exposure there were indications that the rate of decline in heart rate was levelling off relative to the controls.



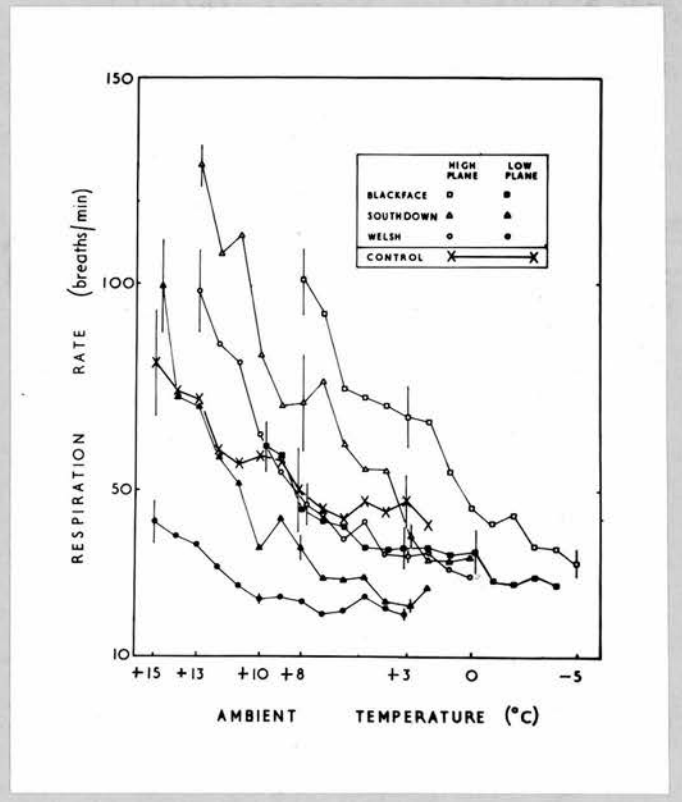


Fig. 21. The changes in (a) mean heart rate and (b) mean respiration rate of the 6 groups of sheep during cold exposure. The changes in mean heart rate and respiration of the control sheep are also plotted at 30 min. intervals between 10.30 and 17.00 hrs. commencing on the extreme left of the graph at 10.30 hrs.

6. Respiration rate

The mean respiration rate of control sheep, (Fig. 21) fell by 40/min. ($P < 0.001$) during the $4\frac{1}{2}$ hrs. that measurements were made after the fixing of equipment, and thereafter remained fairly steady at 45/min. With the exception of the low plane Blackface and Welsh sheep a greater fall in respiration rate was observed in the treated groups. The mean final respiration rates of all treated sheep were between 20 and 32/min. Thus, although much of the change in respiration rate was probably attributable to a decay of emotional disturbance, some effect of temperature was apparent. At the beginning of exposure, respiration rates of high plane sheep were higher than those of low plane sheep ($P < 0.001$), while the rates for both high and low plane Southdown sheep were higher than those of comparable Welsh and Blackface sheep ($P < 0.05$ in all cases), which did not differ significantly from each other. The degree of elevation of respiration rate at the "thermoneutral" temperature probably reflects the extent to which the sheep were above their critical temperature. As judged by the subsequent onset of vasoconstriction, Blackface and Welsh sheep were approximately 8°C and Southdown sheep 11°C above their respective critical temperatures at this time.

DISCUSSION

The introduction of untrained sheep to the climate chamber environment inevitably resulted in considerable emotional disturbances which were most apparent after handling. Hence, presumably, the falls in rectal temperature, heart rate and respiration rate which were observed soon after the fixing of equipment in control and treated sheep. The extent of these changes in control sheep - rectal temperature fell by 0.4°C, heart rate by 15 beats/min. and respiration rate by 40 min. between 10.30 and 12.30 hrs. and the tendency for light vasoconstriction to occur in some sheep after being undisturbed for several hours - suggests that, initially, the heat production of the treated sheep was abnormally high. Emotional effects varied between individuals. Some sheep, especially those on low plane nutrition, showed an initial vasoconstriction in the ears or feet which was gradually relaxed. Others showed high rectal temperatures, heart rates and respiration rates, but no vasoconstriction. It seems probable that, in the latter sheep, the initial reaction on disturbance may have been peripheral vasoconstriction which, after movement and a consequent increase in heat production, was overridden by the need to dissipate heat.

In general, there was a good relationship within individual sheep in the environmental temperatures at which ears and feet vasoconstricted. However, when the sheep were subsequently shorn (Section A) the ears consistently vasoconstricted at a higher ambient temperature than the feet. Although actual ear and foot skin temperatures at vasoconstriction were considerably lower in unshorn compared with shorn sheep, (see Tables 5, 19 and 34), the differential between ears and feet remained. That is, ear

temperature was 3-4°C higher, on average, than foot temperature at vasoconstriction. Similar variation in skin temperature at the onset of vasoconstriction between extremities was observed in calves by Gonzalez-Jiminez and Blaxter (1962). Slee (1968) has also found that while ears and feet of sheep in full fleece vasoconstrict at similar ambient temperatures, vasoconstriction occurs later in the feet after shearing. During shearing of the present sheep care was taken to remove as much hair and wool from the ears and feet as possible. It could be argued for the Southdown sheep, which have a thick fleece cover on the face and around the ears, that shearing may have removed a relatively greater amount of external insulation from the ears than from the feet. But this would certainly not be the case for the two hill breeds which had no fleece cover on the face. The reason for this difference in response between unshorn and shorn sheep is not clear.

The faster rate of cooling of the ears compared to the feet after vasoconstriction, shown also by the shorn sheep, may be related to differences in their surface area/volume relationship. Heat loss is related to surface area, and heat storage capacity to volume. The feet, being cylindrical, probably have a relatively larger volume and smaller surface area than the ears, and should therefore lose heat less rapidly after vasoconstriction. The possibility that variation in the completeness of vasoconstriction and in the anatomical arrangement of blood vessels contributed to the differences cannot, however, be discounted.

Predictably fleece length and food consumption (both the general feeding level and the recent food consumption) had a large influence on vasomotor responses. Fig. 22a, which is adapted from the data of Armstrong et al. (1960), shows their calorimetric determinations of critical

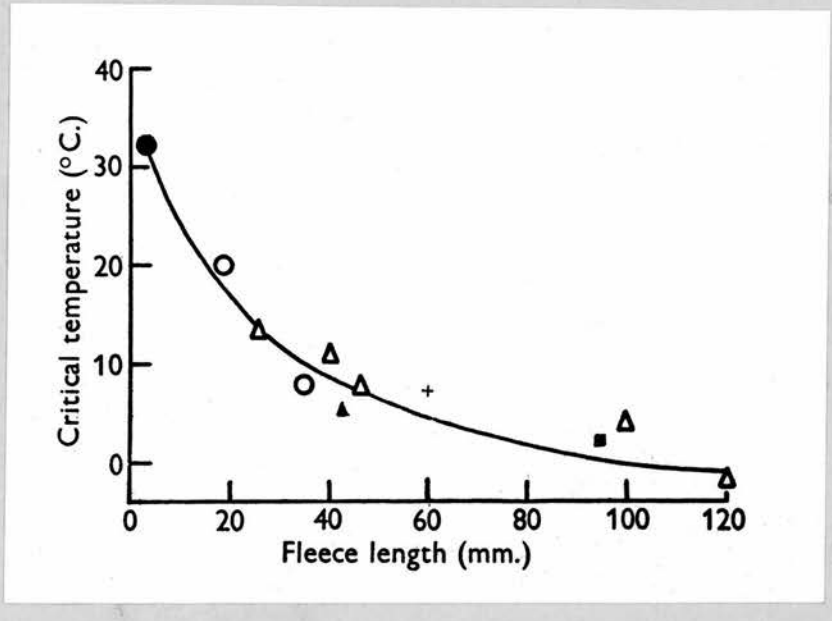


Fig. 22a This figure is adapted from the data of Armstrong et al. (1960) and shows the critical temperatures of sheep on maintenance levels of nutrition estimated by calorimetric determinations of heat production (● = mean of down cross and mountain breeds, O = mountain breeds, = down cross breeds). Superimposed are the present values for critical temperature based on vasomotor responses (■ = Blackface, ▲ = Southdown, + = Welsh breeds)

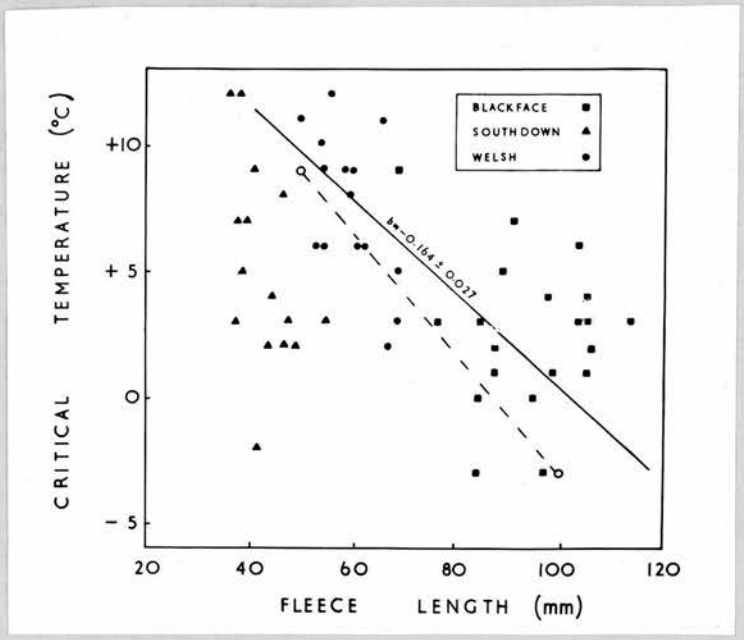


Fig. 22b The relationship between critical temperature (estimated from vasomotor responses) and fleece length in low plane Blackface, Southdown and Welsh sheep. Values given by Blaxter (1962) are also plotted (O---O).

temperature for hill and down cross breeds of sheep, together with the critical temperatures of the present Blackface, Southdown and Welsh sheep estimated from vasomotor responses - both plotted against fleece length. All the sheep were on maintenance levels of nutrition. The present estimates of critical temperature can be seen to give reasonably good agreement with those of Armstrong et al. The hill breeds (Blackface and Welsh) tended to vasoconstrict slightly earlier and the Southdowns slightly later than would be predicted from the calorimetric data. The results for the Southdown sheep may be explained partly by a slightly higher food intake on the day of the test but mainly by their greater fleece cover on the ears and feet which would reduce cold stimuli.

Similarly, Fig. 22b, in which the estimated critical temperature is plotted against fleece length for low plane sheep, does show that Southdown sheep lie outside the fitted line for the Blackface and Welsh data. In relation to their fleece length Southdown sheep had a compartively low critical temperature. On the basis of calorimetric determinations of heat production and heat loss, Blaxter (1962) derived a general formula for prediction of the critical temperatures of sheep. Substituting his own values in the formula, he gave the critical temperatures of sheep on a maintenance level of nutrition with 5 cm. and 10 cm. fleeces to be +9°C and -3°C respectively. His work has mainly involved hill and down cross sheep which probably had a fleece morphology comparable to the present Blackface and Welsh sheep. Certainly the gradient of the line joining Blaxter's points is similar to the fitted line for the low plane Blackface and Welsh data (see Fig. 22b). The difference in elevation may be expected on the basis that the metabolic response, which determines the critical temperature, follows the vasomotor response. It seems unlikely that the difference

between the hill and Southdown breeds could be explained by a greater insulation per unit depth of fleece in the Southdown sheep. The sheep were tested under still air conditions, and the insulation of the fleece is considered to be related to the depth of still air which it traps (Blaxter 1962). Moreover, Clapperton et al. (1960) who compared the fleece insulation of Blackface and Cheviot sheep, also under still air conditions, found no difference between breeds at a given fleece length. Slee, (1964 and 1968), who compared the vasomotor responses of Blackface and Merino sheep, found that vasoconstriction in the Merinos, with a similar fleece morphology to the Southdowns, occurred at a relatively lower temperature than would be predicted from differences in fleece length between the two breeds. He attributed this to their greater fleece cover on the ears and feet.

Whether the relationship between vasomotor and metabolic responses are the same in the Southdown as in the hill breeds cannot be ascertained, since none of the sheep showed any increase in heart rate. Doubts as to the rigidity of the relationship led Barnett and Mount (1967) to suggest that it may be better to use two critical temperatures, one based on vasomotor and the other on metabolic responses. On the present evidence it would appear that vasomotor responses may be useful indices of variation in critical temperature within breeds of sheep. But their validity in comparisons between breeds, where factors such as fleece morphology may complicate the relationship, needs to be tested.

Evidence for adaptation of the three breeds of sheep to their natural habitats is difficult to assess. Blackface sheep had longer and heavier fleeces, were heavier than the other two breeds and therefore had lower actual critical temperatures. At any subcritical environmental temperature

their energy expenditure necessary to maintain body temperature would presumably be lower than that of the other two breeds. One might reasonably expect to find adaptive features favouring cold tolerance in the two hill breeds by comparison with the down breed. Apart from having longer and heavier fleeces the feature peculiar to the hill breeds was an absence of wool cover on the face, ears and feet. The significance of this as an adaptive feature is not clear. In wet conditions more water might be lost directly from these areas as run-off when hair covered with a consequently smaller need for heat loss by evaporation. Judging by the recent evidence of Blaxter, Clapperton and Wainman (1966), variation between breeds of sheep supposedly adapted to different climates and with different fleece types may be greatest in response to components of climate other than temperature, such as wind and rain. However, in this and in other studies the extent to which artificial and natural selection have contributed to the phenotype under study cannot be assessed.

SUMMARY

The vasomotor responses of unshorn Blackface, Southdown and Welsh sheep under mild cold exposure were compared. The evidence from changes in rectal temperature, heart rate and respiration rate showed that handling the sheep soon after their introduction to the climate chamber caused some emotional disturbance. These may have affected the absolute values obtained, but did not appear to influence comparisons between breeds.

A high correlation was found within individuals between the ambient temperatures at which the ears and feet vasoconstricted. Significant relationships were established between fleece length, food consumption and the critical temperature. Critical temperature, defined as the ambient temperature obtaining when both extremities had vasoconstricted, was lowest in the Blackface sheep which had the longest and heaviest fleeces and were heavier than the other two breeds. Average estimated critical temperatures were +1°C, +3°C and +7°C for the Blackface, Southdown and Welsh sheep respectively, those for high plane sheep being approximately 2°C lower than for comparable low plane sheep. Southdown sheep, by comparison with the two hill breeds, appeared to have a rather low critical temperature relative to their fleece length, fleece weight and bodyweight. This was considered to be due to their more comprehensive fleece cover on the face, ears and feet.

However, the generally good agreement which was obtained between the present estimates of critical temperature based on vasomotor responses, and those of other workers in which calorimetric determinations of heat production were made, suggests that vasomotor responses may be useful indices of the variation in critical temperature within breeds. Their validity for comparisons between breeds may be questionable in unshorn sheep.

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APPENDIX 1.

Ration Composition

K.31 special sheep pencils developed by Mr. H. B. Carter and supplied by B.O.C.M.

	%
Groundnut Meal	10
White Fish Meal	7
Lime	1
Oatfeed	70
Exp. Linseed Cake	12
Ascorbic Acid	10 gms.
Vitamin Supplement	200 gms.

Oil	S.E.	D.C.P.	Fibre
3.4%	36.4%	13.8%	17%

APPENDIX 2.

Papers published during the course of the work

Reprinted from ANIMAL PRODUCTION, Vol. 9 Part 3, pp. 333-347, August 1967

ACCLIMATISATION OF SCOTTISH BLACKFACE SHEEP TO COLD

1. RECTAL TEMPERATURE RESPONSES

J. SLEE AND A. R. SYKES†

A.R.C. Animal Breeding Research Organisation, Edinburgh, 9

COLD acclimatisation has long been recognised in birds and rodents (Hart, 1957 and 1963). It has usually implied an extension of the animal's survival time at a specified low temperature, or a depression in the lethal temperature.

Cold acclimatisation in man is less clearly established. Some workers, for example Adolph and Molnar (1946), Horvath, Freedman and Golden (1947) and Leblanc (1956), found no clear evidence for it. But more recently Glaser (1950), Glaser and Shephard (1963), Budd (1962 and 1964) and Davis (1961 and 1963) have reported different forms of cold acclimatisation in man. Disparity may have resulted from differences in the methods used. These varied from long exposures of clothed men in fluctuating outdoor environments to short exposures of nude subjects in controlled temperature rooms.

So far there has been no evidence for the occurrence of cold acclimatisation in farm animals. However, any ability to acclimatise would seem important for the hill sheep in its natural habitat and relevant for the sheep physiologist who may use the same sheep successively to measure the effects of different types of cold exposure. In the present experiments the cold resistance of sheep was determined by their degree of success in maintaining rectal temperature during severe cold exposure. It was assumed that improved cold resistance, resulting from previous exposures to cold temperatures, could be used as a measure of acclimatisation. These experiments are concerned solely with acclimatisation in the laboratory, as distinct from natural acclimatisation which may occur in the field as a result of fluctuations in several climatic factors.

The results show that Scottish Blackface sheep, at least, are capable of cold acclimatisation under certain conditions.

MATERIAL AND METHODS

Forty-eight Scottish Blackface female lambs, born in April 1965, were used. Twenty-nine came from an Animal Breeding Research Organisation hill farm in Peeblesshire; of these, 14 were from a group of sheep selected since 1955 for high fleece medullation and 15 from a corresponding low medullation group (Pilkington and Purser, 1958 and Purser, 1967). The remaining 19 sheep were similar but drawn from a random bred flock on a lowland farm. All sheep were brought indoors on 25 October, 1965, and fed individually on a high-protein pelleted cake. They were equally divided into groups for high- and low-plane nutrition and subsequent temperature treatment. Between groups there was an even distribution with respect to farm of origin, fleece selection type, and bodyweights on 8 November. The basic high- and low-plane rations were 36 and 23 g./kg. body weight/day respectively, calculated from individual body weights on 8 November. While the low plane ration remained constant throughout, the daily high plane ration

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ACCLIMATISATION OF SCOTTISH BLACKFACE SHEEP TO COLD

1. RECTAL TEMPERATURE RESPONSES

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COLD acclimatisation has long been recognised in birds and rodents (Hart, 1957 and 1963). It has usually implied an extension of the animal's survival time at a specified low temperature, or a depression in the lethal temperature.

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was increased each week by 30 g./head until the beginning of cold treatment, when it was stabilised. The low and high plane sheep were then consuming on average 630 g./day and 1,300 g./day respectively.

A series of double cold exposures commenced on 12 January. The day before the first cold exposure (day 1) each sheep was closely clipped to leave approximately 3–4 mm. of wool. Immediately after clipping and before 17.00 hr. the sheep entered the climate chambers, where the temperature was +30° C.—estimated as thermoneutral for the shorn sheep from the data of Blaxter, Graham and Wainman (1959) and Armstrong, Blaxter, Clapperton, Graham and Wainman (1960). Next morning (day 2) thermocouples were attached at 08.00 hr., and recordings began at 09.30 hr. when room temperature was still at +30° C. The sheep had then been allowed at least 16 hours to adjust emotionally and physiologically to the new environment.

TABLE 1

Experimental plan

Treatment groups	Day 1	Day 2	Days 3–14	Day 15	Day 16
HP30	Entered chambers at +30° C.	1st acute cold exposure	Kept at +30° C.	——→	2nd acute cold exposure
HP8	,,	,,	kept at +8° C.	chamber temperature raised to +30° C.	,,
LP8	,,	,,	kept at +8° C.		,,
LP30	,, Shorn	,,	kept at +30° C. Re-shorn	——→ Re-shorn	,,

HP = high plane nutrition. LP = low plane nutrition.

Measurements were taken for 1 hour at +30° C. before a controlled decrease in room temperature at a rate of 1° C. per 5 minutes began. This continued for 2½ hours until room temperature reached 0° C. at 13.00 hr. Then small individual fans, providing a 4 m.p.h. wind at the midside of each sheep, were switched on, and room temperature was lowered to reach −12° C. at 13.30 hr., −15° C. at 14.00 hr., −18° C. at 15.00 hr. and −20° C. at 17.00 hr. Exposures were terminated individually after 8 hours exposure from 13.00 hr. or when rectal temperature had fallen to 37·5° C. After this acute cold exposure the sheep received one of two alternative treatments. Under one treatment they spent the next 2 weeks at +30° C. (these are referred to as HP30 and LP30 groups); for the other treatment they were first allowed to recover for 12 hr. at +20° C. and then remained for 2 weeks at +8° C. (HP8 and LP8 groups). On day 15 at 14.30 hr. room temperature for the HP8 and LP8 groups was raised to +30° C. On day 16 all sheep were subjected to a second identical cold exposure, the HP8 and LP8 sheep having then had about 18 hours to re-equilibrate to a thermoneutral temperature. The procedure is summarised in Table 1. Rectal temperatures were measured at the beginning and the end of the constant temperature periods (on days 4 and 14) from 10.30 hr. to 14.30 hr. on each day, as well as throughout the cold exposure days (2 and 16). Copper-constantan 32 swg. thermocouples, inserted 13 cm. and connected to a Honeywell-Brown chart recorder, were used.

During the period of cold treatment there were minor modifications in the feeding regime. All the sheep received maintenance rations on days 1 and 15, no food on days 2 and 16 until after cold exposure, and half maintenance rations before temperature measurements on days 4 and 14. After measurements were completed on days 4 and 14 the rations were made up to the appropriate high and low plane levels. On day 3 and the other intervening days between cold exposures, normal high- and low-plane rations were fed. The intention was to maintain the established high- and low-plane differential except on the days when physiological measurements were taken when the sheep were either fasted or fed equal rations. The sheep were reclipped closely on days 11 and 15.

Twenty-four sheep (6 per treatment group) were treated as described above. Eight more sheep (2 per treatment group) were treated similarly except that both their acute cold exposures were slightly (but equally) less severe than the standard exposure—due to technical difficulties with refrigeration. Data from these sheep are included in all calculations except those for Figure 1 where rectal temperatures have been extrapolated. Eight other sheep (2 per treatment group) were clipped and spent two weeks in the climate chambers at the thermoneutral temperature of +30° C. before receiving their first cold exposure. The intention here was to test whether performance under cold exposure could be influenced by habituation to the climate chamber environment. These sheep, the habituation controls, were treated according to the normal procedure from the time of their first cold exposure onwards, and data derived from them were used in the main analysis. Finally, eight more sheep (6 on high-plane and 2 on low-plane nutrition) were clipped and spent two weeks at +8° C. before the first acute cold exposure. These sheep were kept at +30° C. between the first cold exposure and the second one two weeks later. This treatment was intended to show whether performance under cold exposure could be influenced by chronic moderate cold in the absence of previous acute cold exposure.

Analysis

The resistance of sheep to cold has been assessed by measuring the rate of decline of rectal temperature (in °C. per 100 min.) during exposure to a standard cold environment. Thus it was possible to compare directly sheep whose exposure was terminated when rectal temperature had fallen to 37·5° C. with those showing little or no depression after 8 hr. exposure.

In measuring the rate of decline of rectal temperature two problems emerge. First, should the rather variable normal temperature of the individual sheep be considered as the baseline from which the temperature depression is measured, or are the length of cold exposure and the actual rectal temperature after exposure the only important parameters? For example, is there a physiological difference between a sheep with an initial rectal temperature of 40·0° C. falling to 39·0° C. during exposure, and one whose rectal temperature falls from 39·5° C. to 39·0° C.? One rate of decline is twice the other but each has the same final status. Secondly, if the initial temperature is to be considered, how should it be estimated? The initial (presumably normal) rectal temperatures of our animals, measured before treatment, varied considerably between sheep and, at different times, within the same sheep. The causes of this variation were not always clear, but it was apparently unrelated to subsequent performance. On the assumption that the

final rectal temperature at the end of exposure and the total time of exposure were the significant parameters, the rates of decline were computed from a standard of 39·7° C. This was the mean rectal temperature of all sheep measured at the same time of day in a thermoneutral environment before the experimental temperature treatment began. This procedure has been followed throughout unless otherwise stated. In a few exceptional cases, where indicated, the rate of decline was calculated from the actual rectal temperature obtaining at 13.00 hr. just before the acute (sub-zero) period of cold exposure commenced (see Figure 1). As an additional check, rates of decline were also computed using individual pre-treatment rectal temperatures measured in a thermoneutral environment. These data are not presented. However, all the major findings and the levels of significance between treatment groups, when examined under each of these possible criteria, remained substantially the same.

Statistical differences were calculated by *t* tests on paired differences within individuals where possible, or by conventional *t* tests, and by analysis of variance.

The term 'performance' refers in the text to the rate of decline of rectal temperature of any sheep or group of sheep. Good or improved performance indicates a low or decreased rate of decline of rectal temperature under cold exposure.

RESULTS

There were no significant differences in performance between those sheep from different farms or those previously selected for differences in fleece type. Data from these classes of sheep have therefore been pooled. The results centre mainly on a comparison between sheep in the four main treatment groups designated throughout as: HP8, HP30, LP8 and LP30 according to the plane of nutrition and the ambient temperature maintained between the two acute cold exposures.

Rectal temperature during cold exposure

Table 2 shows the performances of sheep on first and second cold exposure, classified into three categories. The proportion of sheep surviving the full exposure period without showing the maximum permitted decline in rectal temperature was clearly increased on the second exposure ($P < 0{\cdot}001$ for all treatment groups combined). The resulting changes in frequency ratio were most marked in the HP8 group and least apparent in the LP30 group.

For a quantitative comparison of all sheep the mean overall rates of decline in rectal temperature are given in Table 3. These show a highly significant improvement in the ability of all groups of sheep to maintain rectal temperature at the second cold exposure. High plane sheep showed slower rates of cooling than low plane sheep at both the first ($P < 0{\cdot}02$) and second ($P < 0{\cdot}01$) exposures. HP8 and LP8 sheep showed, on average, a greater improvement in performance than HP30 and LP30 sheep, but these differences were not significant. Analysis of variance showed that exposure occasion ($F = 19{\cdot}1, P < 0{\cdot}001$) and plane of nutrition ($F = 13{\cdot}4, P < 0{\cdot}001$) had most influence on performance. The short acute cold treatment of the first exposure apparently had more effect on subsequent performance than the prolonged period of moderate cold between exposures; or the acute effect

was sufficiently large to mask that due to the moderate cold treatment. The effect of acute cold exposure on subsequent performance was also apparently greater than that of plane of nutrition.

TABLE 2

Performance classification and terminal rates of cooling. Mean decline in rectal temperature during final ½ hr. of exposure (° C.) *and number of sheep involved* (n)

eatment group		1 No temperature decline		2 Decline less than maximum allowed		3 Maximum decline to 37·5° C.		Maximum decline to 37·5° C. on both 1st and 2nd exposures	
		n	Mean terminal decline	n	Mean terminal decline	n	Mean terminal decline	n	Mean terminal decline
;	1st exposure	0	—	3	0·40	7	1·06	1	1·50
	2nd exposure	2	0·00	7	0·13	1	0·80		0·80
30	1st exposure	1	0·00	2	0·25	7	1·10	3	1·20
	2nd exposure	2	0·00	5	0·04	3	0·83		0·83
	1st exposure	0	—	0	—	10	0·77	5	0·88
	2nd exposure	1	0·00	4	0·17	5	0·44		0·44
0	1st exposure	1	0·00	0	—	9	0·68	6	0·63
	2nd exposure	1	0·00	3	0·30	6	0·53		0·53

Changes in mean rectal temperature during cold exposure are shown in Figure 1. Some sections of the graph involve extrapolation, such that from the end of each individual exposure period extrapolated values for that sheep are incorporated in the group mean. Extrapolation has been used only for the data in this diagram. The procedure seemed justified for comparative purposes on the evidence of Slee (1966) and Slee and Wiener (unpublished), showing that in sheep under identical experimental conditions rectal temperature once below 38° C. continued to fall smoothly at a steady or slightly increasing rate. The marked increase in ability to resist body cooling at the second cold exposure is again apparent in Figure 1. Mean final rectal temperatures were significantly higher on the second occasion in each group except LP30. Cooling resistance increased because normal rectal temperatures were sustained longer and also because temperatures subsequently fell more slowly. That terminal rates of decline of rectal temperature were slower on second exposure is clear from Table 2. The difference is highly significant taken over all performance categories and is still apparent ($P < 0{\cdot}02$) even when sheep with the poorest performances are selected for comparison (i.e. those showing maximum cooling to 37·5° C. on both occasions). Finally, it was found that the high plane sheep, despite their significantly greater overall cooling resistance at both exposures (Table 3), nevertheless showed faster terminal rates of cooling than the low plane sheep (Table 2; $P < 0{\cdot}001$).

TABLE 3

Resistance to cooling—main treatment groups. Mean rates of decline of rectal temperature (° C./100 min. cold exposure), calculated:

(a) *from a standard rectal temperature of* 39·7 °C. (b) *from actual individual rectal temperatures at* 13.00 *hr.*

Treatment group	N	(a) 1st exposure	(a) 2nd exposure	(a) Significance of difference between 1st and 2nd exposures P	(a) Rate of decline of rectal temperature at 2nd exposure compared with 1st exposure (%)	(b) 1st exposure	(b) 2nd exposure	(b) Significance of difference between 1st and 2nd exposures P	(b) Rate of decline of rectal temperature at 2nd exposure compared with 1st exposure (%)
HP8	10	0·360 ±0·053	0·055 ±0·035	<0·001	15·3 †	0·544 ±0·093	0·012 ±0·055	<0·001	2·2 †
HP30	10	0·296 ±0·071	0·144 ±0·064	= 0·006	48·7	0·492 ±0·141	0·232 ±0·102	= 0·006	47·1
LP8	10	0·483 ±0·027	0·276 ±0·073	= 0·009	57·2	0·771 ±0·070	0·322 ±0·108	= 0·003	41·7
LP30	10	0·440 ±0·078	0·315 ±0·084	= 0·012	71·7	0·737 ±0·134	0·510 ±0·123	= 0·016	69·1

† The disproportionately large increase in cold resistance of the HP8 sheep on these scales of measurement is partly due to the greater number of sheep showing nil or very small depressions of rectal temperature on second exposure (see Table 1). A threshold effect is probably involved, such that longer exposure periods, if used, might have induced proportionately greater increments of temperature decline in the sheep showing most cold resistance on the present scale (i.e. those sheep which remained on the non-inflected sections of the temperature response curves in Figure 1).

At 30° C. room temperature, before the first cold exposure commenced, there were no differences between treatment groups in mean rectal temperature (see Figure 2). However, under the same conditions before the second cold exposure, rectal temperatures of the HP8 and LP8 sheep were higher ($P < 0{\cdot}01$) than those of the HP30 and LP30 sheep. During first exposures, as ambient temperature fell to 0° C., all sheep maintained steady rectal temperatures. During second exposures the HP30 and LP30 sheep again showed no change in rectal temperature during this period.

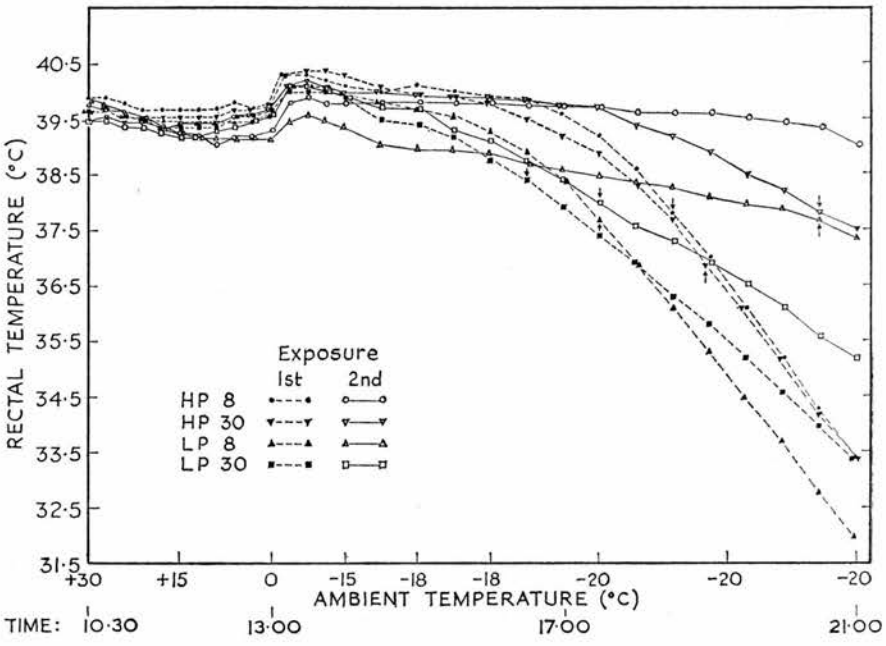

FIG. 1. The pattern of change in mean rectal temperature in the four main treatment groups during both acute cold exposures. Ambient temperature was lowered progressively according to the time scale shown. Arrows indicate the point on each line where extrapolation became necessary for two or more of the eight sheep per group.

But the rectal temperatures of the HP8 and LP8 sheep (Figure 1) showed a gradual decline as ambient temperature fell from +30° C. to +6° C., and at 0° C. were 0·49° C. ($P < 0{\cdot}01$) and 0·44° C. (N.S.) respectively lower on the second than on the first exposure. These sheep had apparently developed a cooling response to moderately subcritical ambient temperatures. To estimate separately the changes in resistance to body cooling under sub-zero exposure, the rates of temperature decline were next calculated from the actual individual temperatures at 13.00 hr. (Table 3). The ratios of second to first exposure performance, and the significance levels of the differences between first and second exposure performance then showed the effects of the intervening 2 week period at +8° C. more clearly than when rectal temperature decline was measured over the whole exposure from 10.30 hr. Analysis of variance on second exposure data showed the effect of temperature reatment between cold exposures to be just significant ($F = 4{\cdot}12$, $P = 0{\cdot}05$). As before, the overall improvement in performance on second exposure was

highly significant. Thus chronic moderate cold treatment and acute cold exposure both influenced subsequent performance under acute cold exposure. Chronic cold treatment also caused a controlled body cooling at moderate ambient temperatures. The effect of high plane nutrition in favouring cold resistance was again significant ($F = 8{\cdot}54$, $P < 0{\cdot}01$).

The immediate response of all sheep to the increased rate of fall in ambient temperature from 0° C. was a rise in rectal temperature to a peak within 30 minutes. There was considerable variation between individuals in the extent of this rise but no significant differences attributable to treatment. The rise tended however to be more pronounced in the high plane sheep.

Twelve sheep, approximately equal numbers from each treatment group, were kept in the chambers at +30° C. for a further 2 weeks after their second acute cold exposure. They then received a third identical cold exposure.

TABLE 4

Resistance to cooling—subsidiary treatment groups

Treatment	N	Mean rates of decline of rectal temperature (° C./100 min.) at first acute cold exposure (±SE)	P<
Habituation control —high plane	4	0·488±0·058	
			0·05
Chronic cold —high plane	6	0·295±0·053	
Habituation control —low plane	4	0·664±0·035	
			0·001
Chronic cold —low plane	2	0·126±0·031	

The mean rates of decline of rectal temperature from 39·7° C. were as follows: 1st exposure: 0·465±0·052; 2nd exposure: 0·243±0·073; 3rd exposure: 0·299±0·069. The majority of sheep showed a slight deterioration in performance from the second to the third exposure but the mean difference was not significant. Sheep showing a large improvement from first to second exposure tended to show most deterioration from second to third exposure and vice versa. The differences between both first and second, and first and third exposures were highly significant ($P < 0{\cdot}001$).

The performance of the 8 habituation control sheep, which were kept in the climate chambers at +30° C. for 2 weeks prior to their first cold exposure, is given in Table 4. The performance of the high plane habituation control sheep was not significantly different from that of comparable sheep which received their first exposure the day after entering the chamber (HP30 and HP8—Table 3). The low plane habituation control sheep showed a slightly poorer performance than the comparable LP30 and LP8 groups ($P < 0{\cdot}01$). This confirms that the improvement in performance shown by the four main treatment groups at the second exposure was an effect of the temperature treatment and was not due to habituation to the chambers. Habituation appeared, if anything, to have had a deleterious effect on performance.

Table 4 also shows the performance of eight sheep subjected to 2 weeks chronic cold exposure at +8° C. before receiving their first acute cold exposure on day 16. These sheep showed a better performance than their habitua-

tion control contemporaries at +30° C., and better also than the main groups of sheep (Table 3), which received their first exposures on day 2. This indicates that sheep may respond to a prolonged period of moderate cold exposure when this treatment is uncomplicated by the effects of acute cold exposure.

Rectal temperature between acute exposures

Figure 2 shows mean rectal temperatures for the four major treatment groups on four occasions: after the sheep had remained undisturbed for 1½ hr. at +30° C. before the first and second cold exposures (i.e. on days 2 and 16 respectively), and on days 4 and 14 between acute exposures, at the treatment temperatures of +30° C. and +8° C.

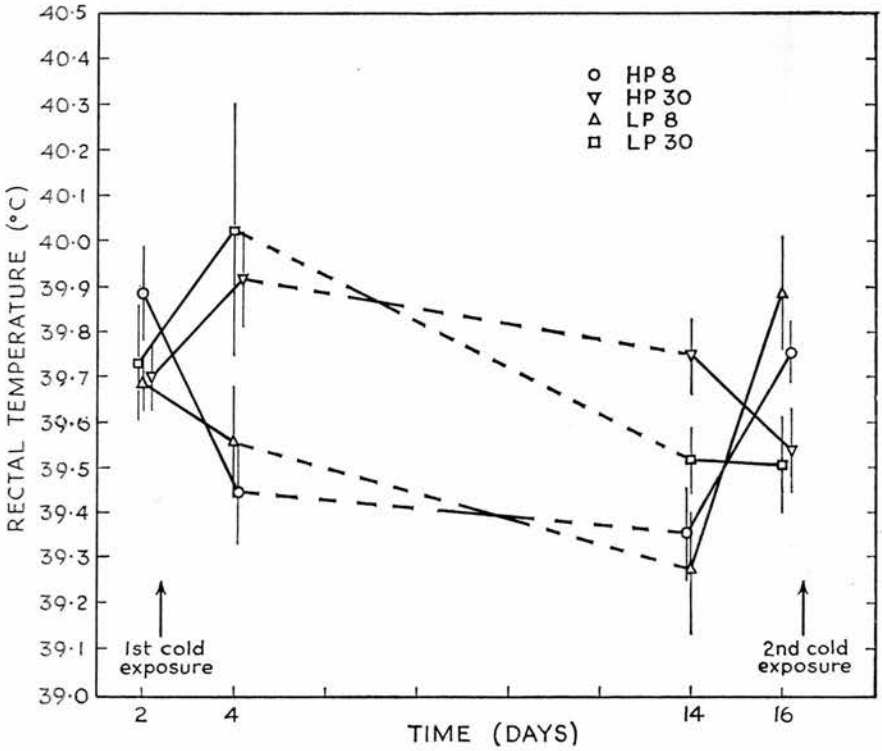

FIG. 2. Mean rectal temperatures in the four main treatment groups (10 sheep per group) before and between acute cold exposures. On days 2 and 16 the ambient temperature was +30° C. for all sheep; on days 4 and 14 the ambient temperatures were +8° C. and +30° C. according to the temperature treatment between acute exposures. Bar lines denote ± 1 standard error.

There were no significant differences between group mean rectal temperatures on day 2. Analysis of variance of data from days 4 and 14 showed that ambient temperature accounted for 18% ($P < 0.001$) and the two exposure occasions for 8% ($P < 0.01$) of the total variation in rectal temperature, while plane of nutrition had no effect. The data for different nutritional planes were therefore combined. The rectal temperatures of HP30 and LP30 sheep were higher ($P < 0.05$) on day 4 than on day 2, whereas those of the HP8 and LP8 sheep had fallen ($P < 0.01$) in the same period, the difference

between +30 and +8 sheep on day 4 being 0·45° C. ($P < 0·01$). The rectal temperatures of both the +30 and +8 sheep showed similar and significant decreases between days 4 and 14 ($P < 0·02$ and $P < 0·05$ respectively). The difference in rectal temperature between the +30 and +8 sheep on day 14 was 0·32° C. ($P < 0·01$). When the +8 sheep were returned to +30° C. before the second cold exposure (day 16) rectal temperatures increased by 0·54° C. ($P < 0·001$) from day 14, and were higher ($P < 0·01$) than those of the +30 sheep. Apparently, therefore, significant changes in rectal temperature resulted from differences in both the prevailing ambient temperature and the previous thermal environment.

Body weight changes and performance

The low plane ration caused mean body weight to remain approximately constant from the time of allocation to treatment until each animal received its first cold exposure, while the high plane ration allowed on average a 30% increase in body weight (Table 5). Between days 1 and 15, 34 out of 40 sheep

TABLE 5

Mean body weight (kg.)

Treatment group	N	8 November 1965	At 1st cold exposure	At 2nd cold exposure
HP8	10	26·7±0·83	34·7±1·24	32·3±1·28
HP30	10	27·0±0·69	33·6±1·22	32·3±1·03
LP8	10	26·5±0·99	27·5±1·10	25·5±0·93
LP30	10	26·9±0·68	27·5±1·01	26·6±0·85

lost weight. The HP30 and LP30 groups combined showed on average 49% of the weight loss of their contemporaries at +8° C. During this period 15 out of 20 high plane sheep refused some food. The amount left was not associated with temperature treatment, weight change, or response to cold exposure. One LP8 sheep refused food and its performance at the second cold exposure was the poorest of the group.

There was no consistent relationship between body weight and cold resistance except in the LP8 sheep at the second cold exposure ($r = +0·82$; $P < 0·01$). At the first exposure, body weight accounted for only 9% of the variation, by regression, in performance of all sheep. However weight gain in the three weeks prior to the first cold exposure was associated with good performance over all treatment groups ($r = +0·47$; $P < 0·01$) and accounted for 22% of the variation in performance.

Variation in performance

Variation in cold resistance at the initial exposure ranged from a rectal temperature change of +0·008 to −0·654° C./100 min. on high plane ($\bar{x} = -0·348$, $CV = 59·8\%$), and from +0·106 to −0·736° C./100 min. exposure on low plane nutrition ($\bar{x} = -0·486$, $CV = 33·2\%$). There was also considerable variation in the extent to which the performance of sheep improved, especially those kept at +8° C. For example in the HP8 group, one sheep showing a rate of fall of 0·417° C./100 min. on the first exposure, actually had an elevated rectal temperature after the second cold exposure; whereas

another in the same group showing an initial rate of fall of 0·488° C./100 min., was only reduced to 0·353° C./100 min. on the second exposure. The most improved LP8 sheep showed a rate of fall reduction from 0·505 to 0·031° C./100 min., whereas 2 sheep actually deteriorated in performance at second exposure. Individual repeatability of performance under cold exposure was quite high for the HP30 and LP30 sheep ($r = +0{\cdot}79$, $P < 0{\cdot}01$; and $r = +0{\cdot}89$, $P < 0{\cdot}001$ respectively); but was not statistically significant for the HP8 and LP8 sheep ($r = +0{\cdot}36$ and $r = +0{\cdot}56$ respectively). Apparently, acute cold treatment caused a uniform improvement in performance, whereas the addition of chronic moderate cold treatment produced a more varied response.

DISCUSSION

The resistance of Blackface ewe hoggs to body cooling has been modified by two types of cold experience, demonstrating that sheep, in common with birds, rodents and possibly man, possess the ability to acclimatise to cold. Acclimatisation caused increased resistance to hypothermia similar to that found in rats by Gelineo (1934), Sellers, Reichman and Thomas (1951), Hart (1953), Cottle and Carlson (1954), Heroux, Hart and Depocas (1956) and others; in the hamster and squirrel by Adolph and Richmond (1956) and in the squirrel by Pohl and Hart (1965). Work on man has not been strictly comparable, although Budd (1964) and Budd and Warhaft (1966) observed an increase in resistance to body cooling of men during a stay in Antarctica.

The immediate response of the sheep to sudden acute cold exposure was a sudden rise in rectal temperature followed by a gradual fall, and this would suggest that in most cases summit metabolic rates were quickly attained. This characteristic rise in rectal temperature on initial cold exposure has been observed in adult sheep by Joyce and Blaxter (1964) and Slee (1966), and in lambs by Alexander (1961). As suggested by Slee (1966) it is probably the result of an overcompensating rise of metabolic rate, coupled possibly with insulative vasomotor changes. Some sheep also showed small periodic fluctuations in rectal temperature during subsequent stages of cold exposure.

The improved cold resistance during second cold exposure resulted from sheep maintaining a near normal body temperature for a longer period of time, and subsequently allowing a slower rate of fall. The HP8 and LP8 sheep began sub-zero cold exposure with a slightly lowered rectal temperature on the second occasion, but were able to maintain this for longer than the HP30 and LP30 sheep. Acclimatised sheep, therefore, by comparison with non-acclimatised sheep, exhibited good overall cold resistance with slow terminal rates of fall of body temperature. Sheep on high plane nutrition, by comparison with those on low plane, showed relatively fast terminal rates of fall, at both first and second exposures, despite their good overall cold resistance. Nevertheless their terminal rates of fall were still less on second exposure than at the first exposure. Possibly the high plane sheep were able to mobilise greater energy reserves initially during exposure, but used them less economically. Hart (1963) states that in rats the total time to death by hypothermia was a two component process depending on the time that metabolic rate could be maintained at summit levels and the time taken for metabolism to fall to zero. It therefore seems probable that sheep, after acclimatisation, could maintain high metabolic rates for longer and then sustain a less rapid decline of metabolism under cold exposure.

Acute sub-zero cold exposure for up to 8 hr. clearly caused acclimatisation in our sheep. Chronic moderate cold exposure (+8° C.) for 2 weeks *without* acute exposure, apparently also produced acclimatisation. The barely significant additional effect of chronic cold exposure demonstrated *after* acute cold exposure suggests that the sheep had almost reached their physiological limit for acclimatisation after one acute exposure. There was no evidence that the degree of acclimatisation after acute exposure was related to the length of exposure or the degree of hypothermia induced. Adolph and Richmond (1956) found in hamsters and squirrels that a few hours gradual cooling of both core and skin was more effective than either prolonged exposure to cool air without deep hypothermia or sudden deep hypothermia. After acclimatisation their animals had an improved initial resistance to cooling, but did not show the subsequently decreased rate of cooling found in our sheep.

Sellers *et al.* (1951) found that, during chronic sub-critical exposure of rats, acclimatisation took 6 weeks to develop and was lost within 4 days. But our sheep showed a quicker development of acclimatisation, like the rats of Gelineo (1934), and some effects of acute exposure persisted for at least 2 weeks. However, the response may have been maximal soon after the first exposure and it is from this point that any degree of retention should be measured. Most sheep tested a third time showed a slight but not significant deterioration from their second exposure performance, only two out of twelve sheep showing any further improvement at the third exposure. Greatest deterioration occurred in those individuals whose resistance had increased most from first to second exposure. These results are difficult to interpret because the second cold exposure not only measured the degree of acclimatisation resulting from the first exposure, but could also itself have caused either a further increase in acclimatisation or a reduction in existing acclimatisation by inducing debility. Nevertheless the evidence suggests that acclimatisation was generally maximal at the second exposure and tending to decline thereafter.

Sheep exposed to sub-critical temperatures (+8° C.) between acute exposures maintained rectal temperature 0·40° C. lower on average than sheep kept at +30° C. The +8 sheep also allowed rectal temperature to fall as ambient temperature decreased from +30° C. to 0° C. on the second acute exposure, while those sheep which had been kept at +30° C. between exposures maintained rectal temperature approximately constant. These findings suggest that the +8 sheep had developed adaptive cooling of the body core. Davis (1963) demonstrated similar rectal temperature responses in humans. Those changes took 14 days to develop compared with 2 days in our sheep, but the conditions of exposure were somewhat different. Glaser (1950) demonstrated a similar effect after 1 day of exposure in humans, although 2 days later rectal temperature had begun to return to normal. Our sheep showed no sign of a return to normal after 10 days. Presumably by reducing the body core/environment temperature gradient they could maintain body temperature more economically. These adaptive cooling responses may be analogous to the seasonal changes in body temperature shown by a sheep in the field (Bligh, Ingram, Keynes and Robinson, 1965).

Rectal temperatures of sheep at +30° C. two days after acute cold exposure were higher than in the same sheep at +30° C. immediately before cold exposure. Also the rectal temperatures of +8 sheep were higher than those

of the +30 sheep when both were measured at +30° C. before the second exposure. According to the evidence of Joyce and Blaxter (1964) thermal equilibrium should have been re-established after the change of temperature. It seems probable therefore, that low temperature exposure had increased the basal metabolic rate of the sheep, as demonstrated in rats by Gelineo (1934), Depocas, Hart and Heroux (1957) and Cottle and Carlson (1954).

In general, rodents undergoing acclimatisation have been fed *ad libitum*, and voluntary feed intake has increased in the cold. The effects of additional energy intake and acclimatisation have therefore been confounded. In our experiment acclimatisation occurred although both high and low plane rations were fixed during the treatment period. However the high plane sheep were able to maintain rectal temperature longer than low plane sheep on both the first and second cold exposures. They also acclimatised slightly more than low plane sheep but not significantly so. Performance at the first cold exposure was more closely related to the gain in body weight over the previous 3 weeks than to actual live-weight. A similar relationship was found over a period of one year by Slee (1966). These findings may be due to sheep which were gaining in weight having greater or more readily available energy stores, and/or thicker layers of subcutaneous fat.

Blair (1951) and Hart (1957) showed that acclimatisation increased the ability to utilise body reserves and so caused weight loss. Most sheep in our experiment lost weight after their cold exposures, but no significant relationship was found between weight change and degree of acclimatisation. Nevertheless, many sheep showed large improvements in performance despite considerable losses in weight. Some low plane sheep losing 20% of their body weight still showed improved performance. Probably, therefore, acclimatisation was associated with increased utilisation of body reserves. Part of the loss in weight of sheep kept at +8° C. may have been the result of decreased body water content.

An important feature of the data was the considerable variation found between sheep of the same sex and breed, and of similar age and weight in their responses to acute cold exposure, despite control of the nutritional and temperature environments throughout the experiment. In addition to the overall variation, there was a tendency for the LP8 sheep in particular to show either considerable acclimatisation or none at all. This raises the question of the optimum cold dosage required for acclimatisation. Possibly some of these sheep had received such a severe cumulative cold exposure that any acclimatisation was obscured by debility. However, the situation may be different when milder doses of cold are used. For example, the data for sheep exposed to chronic moderate cold before the first acute exposure, suggest that then the low plane sheep had acclimatised more than the high plane sheep. Possibly the dosage of cold which induces maximum acclimatisation is dependent on the condition of the individual sheep. The more cold resistant high plane sheep may therefore require a greater dosage of cold to produce maximum acclimatisation.

The most important finding from this work is that, under some conditions at least, sheep can show a marked and rapid acclimatisation to cold temperatures. It follows that in experiments concerning the physiological responses of sheep to cold, particularly when it is important to assess genetic and other sources of variation, then the previous thermal history of the animals may be highly relevant. Moreover, in experiments where the same sheep are subjected

to repeated cold exposures, then the later results may be influenced by previous treatment. Ultimately the considerable individual variation which has been found both in initial cold resistance and in the ability to increase resistance may open up new possibilities for genetic selection on both or either of these criteria. However, further work will be required to establish the heritability of cold resistance and its relevance as a character to performance in the field.

SUMMARY

Closely shorn Scottish Blackface female sheep aged 9–14 months, half on high plane and half on low plane nutrition, were subjected, in climate chambers, to two short acute cold exposures down to −20° C. The exposures were separated by a period of two weeks in either a thermoneutral environment (+30° C.) or a subcritical environment (+8° C.). Thirty-seven out of 40 sheep showed a greater resistance to body cooling at the second exposure. The mean rates of fall of rectal temperature (in ° C. per 100 min. exposure) were 0·42 at the first exposure and 0·22 at the second exposure. One group of sheep showed virtually complete resistance to cooling at second exposure under the specific test conditions used. The highly significant increase in cooling resistance was taken as a measure of acclimatisation.

The main conclusions were as follows:

1. Blackface sheep could acclimatise to cold as a result of one acute exposure to cold lasting about 8 hours.
2. Acclimatisation was slightly greater amongst sheep kept at a subcritical temperature (+8° C.) between acute exposures.
3. Additional data suggested that some acclimatisation resulted from 2 weeks prior exposure to +8° C. alone; but none was induced by 2 weeks prior habituation to the climate chamber environment at +30° C.
4. Sheep on high plane nutrition showed greater initial cold resistance and slightly greater ability to acclimatise than those on low plane nutrition.
5. Cold resistance was more closely related to recent weight gain than to absolute body weight.
6. There was great individual variation in initial cold resistance and in ability to acclimatise.
7. Sheep kept at +8° C. between acute cold exposures maintained significantly lower rectal temperatures than those kept at +30° C.

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ACCLIMATIZATION OF SCOTTISH BLACKFACE SHEEP TO COLD

2. SKIN TEMPERATURE, HEART RATE, RESPIRATION RATE, SHIVERING INTENSITY AND SKINFOLD THICKNESS

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A PREVIOUS paper (Slee and Sykes, 1967) showed that the resistance to body cooling of Scottish Blackface sheep was increased as a result of previous exposure to cold temperatures. This was defined as acclimatization.

When exposed to progressively cooler environments, sheep display the characteristic reactions of homeotherms against hypothermia. These include increases in tissue insulation by vasoconstriction of the extremities as observed by Blaxter, Graham, Wainman and Armstrong (1959), Slee (1964, 1966) and Webster and Blaxter (1966), and increases in heat production involving shivering (Graham, Wainman, Blaxter and Armstrong, 1959).

The present paper describes changes in these physiological reactions during acclimatization. Skin temperature has been used as a parameter related to blood flow and insulation; heart rate and shivering intensity were parameters related to metabolic rate. The changed pattern of these responses was considered as potentially part of the process of acclimatization.

MATERIAL AND METHODS

The basic experimental plan has already been described in detail (Slee and Sykes, 1967), and can be summarized as follows. Thirty-two Scottish Blackface female sheep, aged 9–14 months, were kept indoors for 4–6 months, half on high plane and half on low plane rations. The average high plane ration was initially 970 gm/head per day of pelleted concentrates, increasing by 30 gm/head per day each week; the low plane ration was 630 gm/head per day throughout. The sheep were then subjected to two acute cold exposures 14 days apart. Each cold exposure consisted of an initial controlled lowering of ambient temperature from +30°C (thermoneutral) to 0°C at a rate of 1°C/5 min. A 4 mph wind was then introduced from the right midside of each sheep and ambient temperature was lowered further to reach −20°C 4 hours later. Exposures were terminated individually when rectal temperature had fallen to 37·5°C, or after 8 hr exposure below 0°C. Between the two acute cold exposures half the sheep were kept in a thermoneutral environment (+30°C) and half in a subcritical environment (+8°C). For the latter, ambient temperature was raised to +30°C 18 hr before the second cold exposure began. All sheep were shorn on the day before the first exposure, re-shorn 10 days later and again the day before the second cold exposure. The basic experimental plan is represented in Table 1.

Equipment for recording skin temperature, heart rate, shivering intensity and respiration rate was fixed between 08.00 hr and 09.00 hr on days 2 and 16, and measurements were taken for 1 hour at +30°C before the cold exposures began at 10.30 hr. Skin temperatures were measured on the left midside, left

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ear and the left lower pastern just proximal to the hoof. 32 s.w.g. copper-constantan thermocouples, cemented to depilated skin under small pieces of 'Elastoplast' and connected to a Honeywell-Brown chart recorder, were used. Heart rates were measured by electrocardiograph (ECG) equipment using electrodes attached to the chest wall. They were counted from an audible relay confirmed by oscilloscope display. Counts proceeded over $\frac{1}{2}$ min periods at 15 min intervals from 10.30 hr to 14.00 hr and subsequently at hourly intervals. At the same times shivering intensity was estimated from the activity of the pectoral and biceps femoris muscles using an electromyographic (EMG) technique. Changes in electric potential derived respectively from the chest electrodes and from similar electrodes on the britch were obtained from oscilloscope trace amplitudes converted into millivolts. Gross

TABLE 1

Experimental plan

Treatment groups	Day 1	Day 2	Days 3–14	Day 15	Day 16
HP30	Entered chambers at +30° C	1st acute cold exposure	kept at +30°C →		2nd acute cold exposure
HP8	,,	,,	kept at +8°C	chamber temperature raised to +30°C	,,
LP8	,,	,,	kept at +8°C		,,
LP30	,,	,,	kept at +30°C →		,,
	↑ Shorn		↑ Re-shorn	↑ Re-shorn	

HP = high plane nutrition; LP = low plane nutrition

estimates of shivering were also obtained by direct observation. Respiration rates obtained from thoracic belt, tambour and kymograph equipment were recorded for $\frac{1}{2}$ min periods every 30 min from 10.30 hr until 15.00 hr and subsequently at hourly intervals.

All parameters were measured on days 4 and 14, between the two acute cold exposures, as well as during the exposures on days 2 and 16 (Table 1).

Skinfold thickness, the mean of 2 skin pinches taken on the right midside and measured by 'Harpenden' spring calipers, was recorded on the days preceding the first and the second cold exposure.

In addition to the main experiment, 8 sheep (4 on high and 4 on low plane nutrition) were shorn and kept for 2 weeks at +30°C (thermoneutral) before receiving their first cold exposure. The intention was to test whether cold responses could be influenced by habituation to the climate chamber environment. These sheep, the habituation controls, were treated according to the normal procedure from their first acute cold exposure onwards and they were used in the main analysis. Finally, 8 sheep (6 high plane and 2 low plane) were treated in the same manner, but were kept at +8°C for 2 weeks before their acute cold exposure, in order to test whether their reactions could be modified by chronic moderate cold in the absence of previous cold exposure.

Statistical differences were calculated by *t* tests on paired differences within individuals where possible, or by conventional *t* tests, and, in some cases, by analysis of variance.

RESULTS

Sheep in the four main treatment groups are designated throughout as: HP8, HP30, LP8 and LP30 according to the plane of nutrition and ambient temperature maintained between the two acute cold exposures.

Skin temperature during cold exposures

The changes in mean midside, ear and foot temperatures during first and second cold exposures are shown in Figure 1. Midside temperature fell on average at a rate of 0·35°C/1°C fall in ambient temperature. Rates of fall in individual sheep varied from 0·15°C to 0·55°C/°C. There was no overall

TABLE 2

Significance levels for the differences in mean skin temperature and heart rate at 1st versus 2nd cold exposure

Ambient temperatures and times of measurement	Treatment groups	+30°C (10.30 hr)	+21°C (11.15 hr)	+12°C (12.00 hr)	0°C (13.00 hr)	−15°C (14.00 hr)
Midside temperature	HP8	NS	NS	NS	NS	NS
	HP30	NS	NS	NS	NS	NS
	LP8	NS	NS	NS	NS	NS
	LP30	NS	NS	NS	NS	NS
Ear temperature	HP8	0·01	0·001	0·02	NS	NS
	HP30	NS	NS	NS	NS	*0·02
	LP8	0·05	0·01	NS	NS	NS
	LP30	NS	NS	NS	NS	NS
Foot temperature	HP8	0·001	0·05	0·01	0·02	NS
	HP30	NS	NS	NS	NS	NS
	LP8	0·02	0·001	NS	NS	NS
	LP30	NS	NS	NS	NS	NS
Heart rate	HP8	0·001	0·01	NS	NS	0·01
	HP30	0·05	NS	NS	NS	0·05
	LP8	0·001	NS	NS	NS	0·01
	LP30	NS	NS	NS	NS	NS

Differences are either non-significant (NS) or denoted as the probability of the difference being due to chance.

* With this exception, significance levels derive from differences where second exposure values are the higher.

Note the tendency for significant differences to occur mainly amongst the +8 sheep.

change in thermal circulation index (Burton and Edholm, 1955), nor any consistent evidence to suggest that the midside was capable of vasomotor responses, though at sub-zero temperatures occasional fluctuations of up to 10°C did occur in a few sheep. Midside skin temperatures did not differ significantly between first and second exposures.

At ambient temperatures between +29°C and +21°C on the first exposure vasoconstriction occurred in the ear, and ear temperature fell rapidly until only 5–6°C above ambient temperature. At 0°C ambient temperature, the average ear temperature of all sheep was 5·5±0·63°C. Foot temperatures showed a similar trend, though there was much more variation in the ambient temperature of onset of vasoconstriction, which ranged from +29°C to

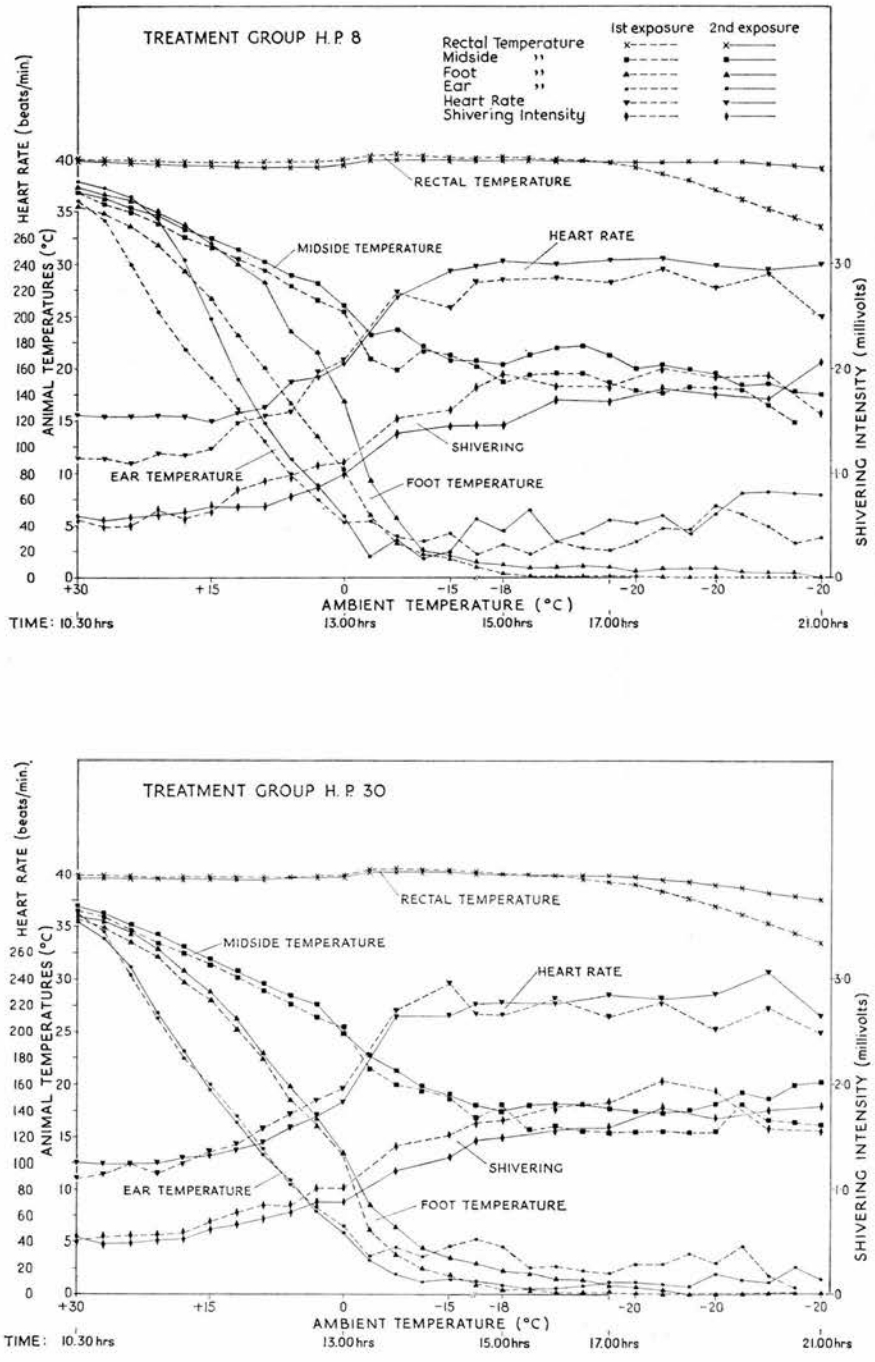
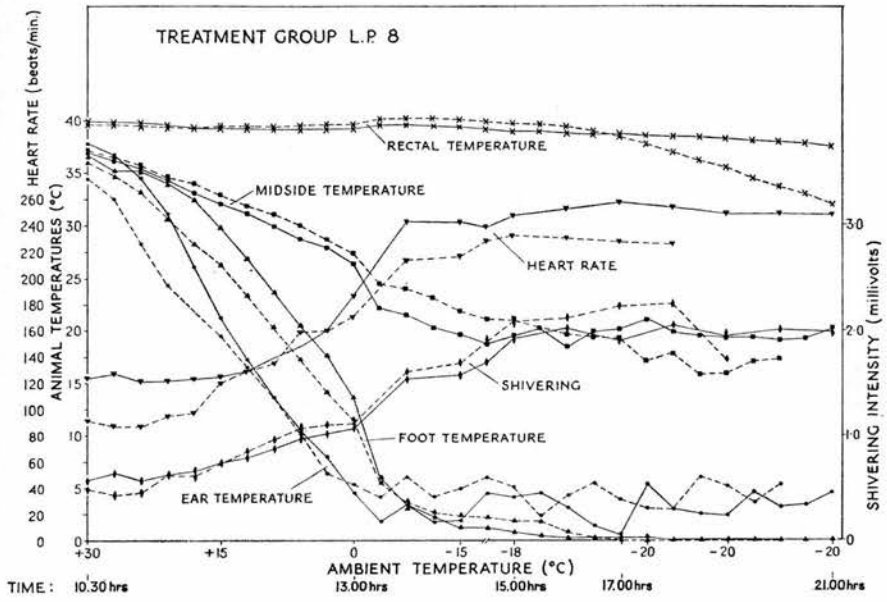
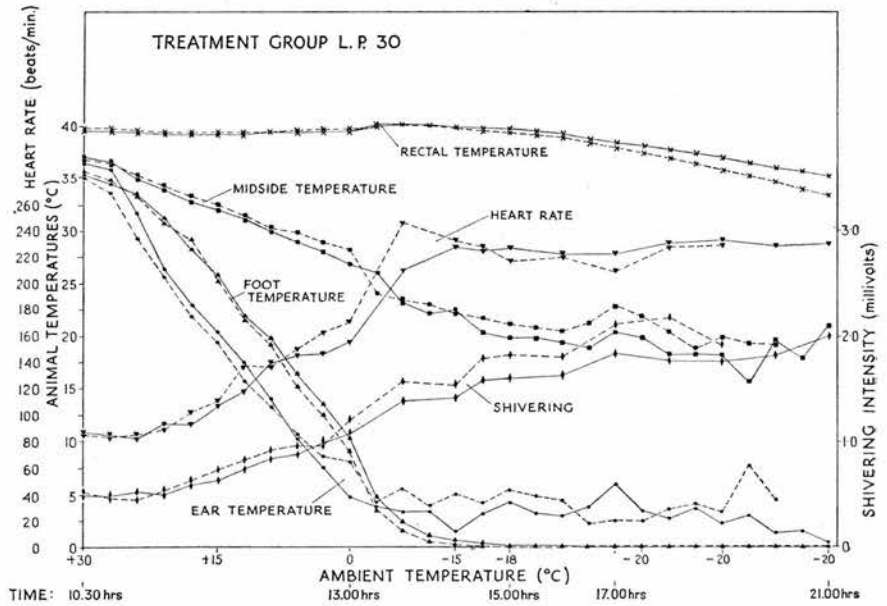


FIG. 1. Changes in mean midside, ear, foot and rectal temperatures, heart rate and shivering in the four main treatment groups (10 sheep per group) during first and second acute cold exposures. Ambient temperature was lowered progressively according to the time scale shown. Rectal temperatures were extrapolated below 37·5°C





(see Slee and Sykes, 1967). Note the tendency for 1st versus 2nd exposure differences in ear and foot temperatures and heart rate to be confined to the HP8 and LP8 groups. Equivalent differences in shivering intensity were common to all treatment groups.

+9°C. After vasoconstriction, foot temperature fell less rapidly than ear temperature, stabilizing about 13°C above ambient temperature, and maintaining this differential as ambient temperature fell to zero. At 0°C the average foot temperature was 11·0±0·72°C.

At the beginning of the second cold exposure, at +30°C, ear temperatures of the HP8 and LP8 sheep were 1·78°C and 3·26°C higher respectively than at the same time on first exposure. Similarly, foot temperatures of these groups were 1·70°C and 1·11°C higher before the second exposure. Significance levels are given in Table 2. There was no significant change in the ear or foot temperatures of the HP30 or LP30 sheep between these occasions. During the second cold exposure, vasoconstriction of the ears and feet of the HP8 and LP8 sheep did not occur until lower ambient temperatures than on first exposure. This resulted in higher foot and ear temperatures at ambient temperatures between +30°C and +12°C (Figure 1a, c). At 0°C ambient temperature these differences had diminished, such that only the foot temperatures of the HP8 sheep were significantly higher on second than on first exposure. Vasoconstriction was slightly delayed in the HP30 and LP30 sheep at the second cold exposure but not enough to produce significant changes in skin temperature.

Under our experimental conditions vasoconstriction occurred whilst both skin temperatures and ambient temperature were falling. The onset of vasoconstriction was defined as the point at which the rate of decline of skin temperature became greater than 0·5°C/5 min (note that ambient temperatures were falling 1°C/5 min). The adoption of this criterion seemed justified by reference to estimated changes in thermal circulation indices. However, in most cases, vasoconstriction was characterized clearly by a sudden change in the rate of fall of skin temperature to a new rate often exceeding 1°C/°C fall in ambient temperature. This was much more marked than is apparent in

TABLE 3

Mean ambient temperature and ear and foot skin temperatures at the onset of vasoconstriction in the ears and feet during 1st and 2nd cold exposures

Treatment group	N	Exposure	Ambient temperature at ear vasoconstriction (°C)	Ear temperature immediately before vasoconstriction (°C)	Ambient temperature at foot vasoconstriction (°C)	Foot temperatu immediate before vasoconstric (°C)
HP8	10	1	26·8±0·70	34·5±0·43	20·0±0·91	31·7±0·5
		2	19·8±1·33	34·9±0·44	10·6±1·51	31·0±0·7
HP30	10	1	25·9±0·81	34·9±0·34	19·7±2·05	31·6±0·8
		2	25·3±1·13	34·1±0·68	13·2±2·38	29·2±0·8
LP8	10	1	27·5±0·53	33·1±0·88	18·3±2·52	30·2±1·1
		2	22·9±1·20	34·7±0·78	15·7±1·55	31·7±0·7
LP30	10	1	27·3±0·60	34·9±0·60	23·2±1·29	32·7±0·7
		2	25·0±1·12	35·2±0·60	19·1±1·73	30·0±1·1

Figure 1, since averaging the data from 10 sheep had a smoothing effect on the curves.

The onset of vasoconstriction with respect to ambient and skin temperatures is shown in Table 3. Analysis of variance of these data showed that the ears of sheep kept at +8°C between exposures vasoconstricted at lower ambient temperatures on second exposure than on first exposure (V.R. = 10·08, $P<0·01$). There was no change in the +30 sheep. Plane of nutrition had no effect. The feet of all groups of sheep vasoconstricted at lower ambient temperatures on second than on first exposure (V.R. = 19·57, $P<0·001$). The extent of this delay in vasoconstriction was similar in the +8 sheep and the +30 sheep. The feet of sheep on high plane nutrition vasoconstricted at lower ambient temperatures than those of low plane sheep, on second exposure only (V.R. = 3·24, $P<0·01$).

Ear and foot temperatures at the onset of vasoconstriction were each very uniform and not influenced by nutritional or temperature treatment (Table 3). However, ear temperatures at vasoconstriction were higher than foot temperatures ($P<0·001$) for all treatment groups at both exposures. There was also a difference between feet and ears in the ambient temperature at which vasoconstriction occurred ($P<0·001$).

Vasoconstriction in the group of sheep kept at +30°C for two weeks before receiving an acute cold exposure (habituation control sheep), occurred at the same ambient temperatures as in the four main treatment groups at their first exposures. However, the group of sheep kept at +8°C for two weeks prior to receiving their first acute cold exposure showed initially warmer extremities and a delay in the onset of vasoconstriction, as did the HP8 and LP8 sheep at the second cold exposure. Consequently, ear temperatures were 2·5°C ($P<0·01$) higher at +30°C; 8·3°C ($P<0·001$) higher at 21°C and 4·0°C (N.S.) higher at 0°C than those of the habituation control sheep. Foot temperatures were 1·5°C, 3·1°C and 2·4°C higher than those of the habituation controls at the same ambient temperatures, but these differences were not statistically significant. Midside temperatures of these groups of sheep were no different from those of the four main treatment groups.

Fluctuations in the temperatures of the feet and ears, termed cold-induced vasodilatation, have previously been observed in sheep at sub-zero temperatures by Webster and Blaxter (1966) and Slee (1966). At temperatures below 0°C our sheep showed spasmodic and rapid increases in ear temperature ranging from 2°C to over 20°C. Fluctuations in foot temperature were rare and never exceeded 4°C. Individual sheep, however, showed vasodilatations of varying magnitude which could not be classified into the two distinct patterns described by Webster and Blaxter (1966). Variation in both number and size of vasodilatations was in fact considerable. The data in Table 4 show that after acclimatization at +8°C there was a general tendency for vasodilatations to increase in amplitude and, in the case of the HP8 sheep, there was an increase in frequency of vasodilatation ($P<0·01$). In contrast, the frequency and magnitude of vasodilatation showed no consistent change in the HP30 and LP30 sheep. The frequency of vasodilatation was apparently independent of body temperature since even when body temperature had been depressed by several degrees, vasodilatation was frequently observed. Rhythmical cycles of vasodilatation, termed by Lewis (1930) the 'hunting reaction' and demonstrated in the ears of sheep by Webster and Blaxter (1966), were rarely observed in our sheep on first exposure but did occur more

TABLE 4

Cold-induced vasodilatations at sub-zero ambient temperatures

Treatment groups	N	Mean total no. of vasodilatations per 100 min exposure		Mean no. of large vasodilatations per 100 min exposure	
		1st Exposure	2nd Exposure	1st Exposure	2nd Exposure
HP8	10	2·32±0·46	4·73±0·12	0·22±0·08	1·05±0·22
HP30	10	3·45±0·41	2·38±0·44	0·36±0·12	0·52±0·16
LP8	10	3·33±0·47	2·87±0·47	0·17±0·09	0·62±0·31
LP30	10	4·22±0·49	2·81±0·61	0·66±0·25	0·56±0·27

Vasodilatations were defined as temporary fluctuations in skin temperature greater than 1·5°C, or, for large vasodilatations, greater than 10°C.

frequently in the HP8 and LP8 sheep at the second cold exposure. Apparently vasodilatation was facilitated by prolonged exposure to a subcritical temperature, and somewhat reduced after prolonged exposure to thermoneutral temperatures. However, these results must be treated with some reserve in view of the considerable variation between groups at the first cold exposure prior to temperature treatment (Table 4).

Skin temperature between cold exposures

There was no difference in midside, ear or foot temperatures on days 4 and 14 due to plane of nutrition, and the data from the two nutritional groups have therefore been pooled (Table 5). The average midside temperature of

TABLE 5

Mean skin temperatures (°C) on the midside, ear and foot between acute cold exposures

Ambient temperature	+30° C		+8° C	
	Day 4	Day 14	Day 4	Day 14
Midside	37·1±0·23	36·8±0·18	29·1±0·46	28·2±0·54
Ear	37·3±0·29	37·0±0·35	12·1±1·01	13·5±1·19
Foot	36·2±0·34	35·4±0·24	17·6±1·89	15·0±1·38

High and low plane nutrition groups were combined.
Each value represents an average based on 20 sheep.

sheep at +8°C was 8°C lower than that of sheep at +30°C, i.e. lower by 0·38°C/°C difference in ambient temperature. There was no change in midside temperature between days 4 and 14.

Ear temperatures of the +8 sheep on days 4 and 14 were depressed rather more than foot temperatures. When compared to sheep at +30°C, the average ear temperature was 25°C lower (1·04°C/°C difference in ambient temperature) and foot temperature 20°C lower (0·89°C/°C). There were no significant changes in foot or ear temperature between days 4 and 14.

Skinfold thickness

Mean skinfold thickness, measured on days 1 and 15 before the first and second acute cold exposures, is shown in Table 6. Chronic cold exposure caused a small, non-significant, increase in skinfold thickness. Wodzicka-Tomaszewska (1960) demonstrated an increase in skin thickness within two hours of cold exposure, and a maximal response within two weeks. Skinfold thickness of her sheep, 4 Merinos and 2 Southdowns, was 2·4 mm initially and showed a 50% increase on exposure to cold and wind. Our sheep had a larger initial mean skinfold thickness and showed only a 10% increase.

TABLE 6

Mean skinfold thickness (mm)

Treatment group	N	Day 1	Day 15
HP8	10	4·1±0·16	4·5±0·40
HP30	10	3·5±0·13	3·5±0·24
LP8	10	3·6±0·16	3·9±0·25
LP30	10	3·3±0·20	3·3±0·17

Heart rate during cold exposure

Heart rates during first and second cold exposures are shown in Figure 1. There were no differences in mean heart rate between groups when measured at +30°C before the first cold exposure. Heart rates of all groups were steady at about 90 beats/min as ambient temperature fell from +30°C to about +20°C, after which they increased linearly, reaching 165 beats/min at 0°C. As ambient temperature fell from 0°C to −15°C heart rates increased rapidly to over 200 beats/min and thereafter remained approximately constant. The heart rates of both HP8 and LP8 sheep were significantly faster at +30°C before the second cold exposure than at the same time before the first exposure (Table 2). During second exposure, however, heart rates showed little change until ambient temperature had fallen much lower (to +9°C and +12°C for the HP8 and LP8 sheep respectively). They then began to increase at the same rate as on first exposure (Figure 1a, c). Heart rates of the +8 sheep were also significantly elevated at sub-zero temperatures during second compared to first exposure. In contrast, heart rates in the +30 sheep were similar during each exposure.

Heart rate between cold exposures

Figure 2 shows mean heart rates recorded on four occasions; after the sheep had remained undisturbed for 1½ hours at +30°C before the first and second acute cold exposure (days 2 and 16) and on days 4 and 14 between acute exposures at the ambient temperatures of +30°C and 8°C. The heart rates of the HP8 and LP8 sheep increased by 36 ($P<0·001$) and 44 ($P<0·001$) beats/min when measured at +8°C on day 4, by comparison with their values at +30°C before the first exposure. The heart rates of the HP30 and LP30 sheep also increased by 20 ($P<0·01$) and 23 ($P<0·01$) beats/min respectively during the same period but measured at +30°C on both occasions. Since

by day 14 the heart rates of the HP30 and LP30 sheep had decreased to their pre-exposure values it seems probable that some effect of the acute cold exposure on metabolic rate was still in evidence on day 4. Rectal temperature (Slee and Sykes, 1967) showed a similarly persistent response.

Heart rate probably is not a completely reliable index of metabolic rate, partly because of its sensitivity to emotional factors. Under our conditions, heart rates were elevated between 09.00 hr and 10.00 hr on experimental days, presumably due to emotional disturbance. But mean heart rates of all sheep measured at a constant ambient temperature of +30°C on day 14 declined only non-significantly from 95 to 85 beats/min between 10.30 hr and 14.30 hr. Apparently, therefore, there were no important emotional effects after

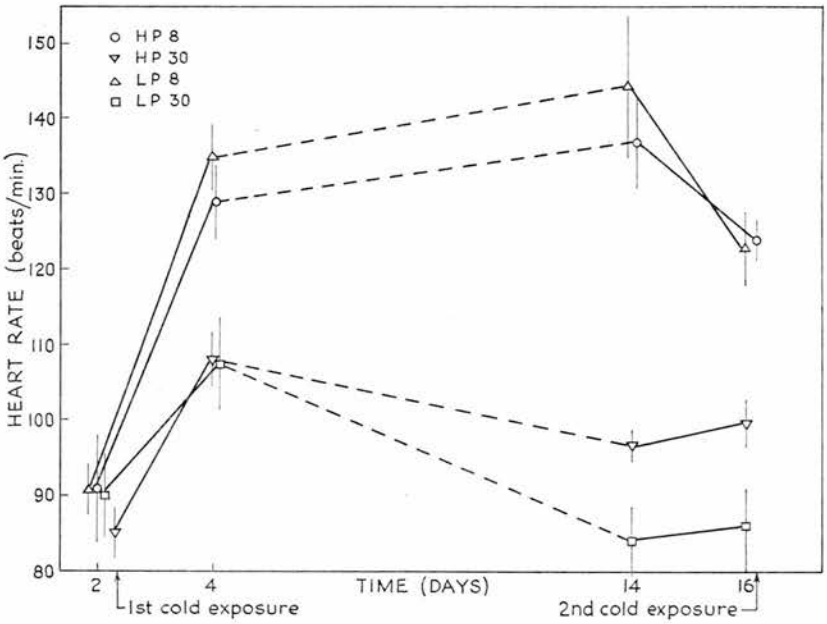


FIG. 2. Mean heart rates in the four main treatment groups (10 sheep per group) before and between acute cold exposures. On days 2 and 16 the ambient temperature was +30°C for all sheep; on days 4 and 14 the ambient temperatures were +8°C and +30°C according to the temperature treatment between acute exposures. Bar lines denote ± one standard error.

10.30 hr during the periods of measurement. Moreover, any emotional factors would tend to maximize heart rates at the beginning of measurement periods, soon after the sheep were disturbed by the fixing of equipment. This would have produced trends opposite to those actually found during cold treatment (Figure 1). Finally, the conclusions drawn from this work depend upon comparisons between groups of animals or between experimental occasions where procedures were carefully standardized and where extraneous factors would be expected to act equally. It therefore seemed reasonable to infer that, in this experiment, *changes* in heart rate were indicative of synchronous changes in metabolic rate within animals and within groups of animals. With regard to this general relationship, Graham (1960–61) observed in sheep a good correlation between change in heart rate and change

in metabolic rate. Booyens and Hervey (1960) also demonstrated a good relationship in men during exercise. Moreover, heart rates do increase when sheep are exposed to cold as a result of shearing (Hutchinson, Bennett and Wodzicka-Tomaszewska, 1960; Wodzicka-Tomaszewska, 1963; and Webster and Lynch, 1966).

We conclude that, in our experiment, where temperature treatment clearly and consistently influenced heart rates, there must have been concomitant changes in metabolic rate. It seems possible therefore that prolonged chronic cold exposure of the HP8 and LP8 sheep had caused an elevation in the basal metabolic rate, as evidenced by the increase in heart rate and in skin and rectal temperature before the second cold exposure. Moreover, while all groups of

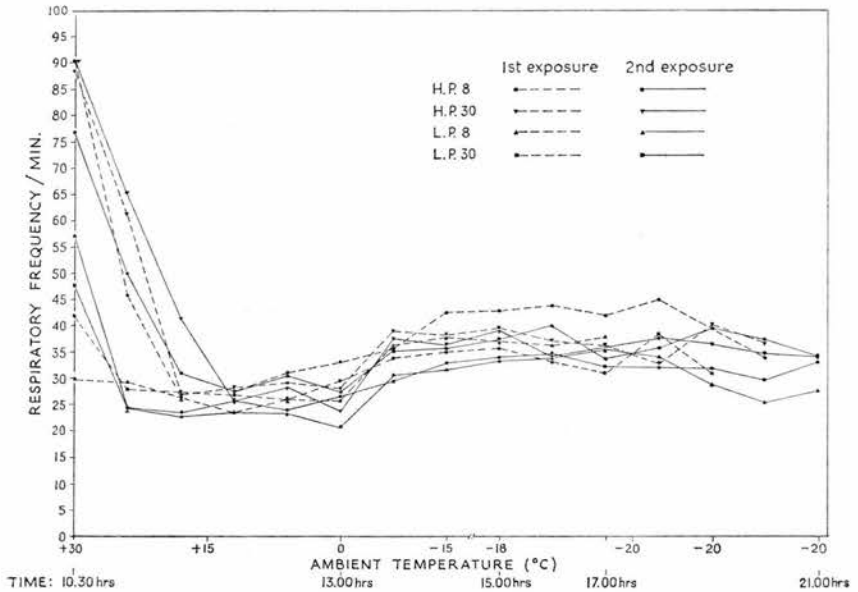


FIG. 3. Mean respiration rates in the four main treatment groups (10 sheep per group) during first and second acute cold exposures. Ambient temperature was lowered progressively according to the time scale shown. From 16.00 hr. the mean values are derives from fewer sheep as individual exposures are terminated.

sheep showed improved resistance to cooling during second cold exposure (Slee and Sykes, 1967) the HP8 and LP8 sheep, those with most elevation in heart rate and skin temperature at sub-zero temperatures, showed relatively more improvement than the HP30 and LP30 sheep. It would appear that their summit metabolic capability under acute sub-zero cold exposure may also have been increased.

Respiration during cold exposure

Changes in mean respiration rate during first and second cold exposures are shown in Figure 3. Respiration rates were variable, but there was a significant difference of 45 respirations/min between the high and low plane sheep at +30°C ($P<0{\cdot}001$). Comparable effects of plane of nutrition upon respiration rate were shown by Blaxter *et al.* (1959). Respiration rates generally decreased as the ambient temperature declined to about +18°C

and heat dissipation in all sheep presumably became minimal. There was little further change in respiration rate as ambient temperature fell from +15°C to 0°C but at sub-zero temperatures a slight increase was observed. There was a slight, non-significant tendency for respiration rates to be lower on second exposure. Tidal volume was not measured directly, but changes in amplitude of pneumograph tracings were considered to indicate changes in tidal volume. During cold exposure mean tidal volume for all groups of sheep, estimated from the trace amplitudes, increased progressively by about 100% as ambient temperature fell from +30°C to −16°C ($P<0.001$). There was no significant difference in tidal volume between first and second cold exposures.

Respiration between cold exposures

Table 7 gives mean respiration rates and tidal volumes on days 4 and 14. High plane sheep generally had higher respiration rates than low plane sheep.

TABLE 7

Mean respiration rates and tidal volumes between acute cold exposures

Treatment groups	N	Respiratory frequency/min		Estimated tidal volume (mm)†	
		Day 4	Day 14	Day 4	Day 14
HP8	10	45·7±9·20	18·9±0·95	1·72±0·43	2·21±0·45
HP30	10	112·9±7·99	121·8±9·15	0·65±0·11	0·94±0·12
LP8	10	32·0±9·91	22·4±2·72	1·70±0·10	2·28±0·33
LP30	10	70·1±7·95	53·3±9·59	1·31±0·18	1·18±0·21

† Tidal volumes were obtained from averaged pneumograph trace amplitudes.

Respiration rates of sheep at +30°C were higher than those of sheep at +8°C ($P<0.001$). There was a tendency for rates to decrease from day 4 to 14 in all groups except the HP30 sheep. Sheep kept at +8°C between exposures had larger tidal volumes than sheep at +30°C ($P<0.001$). Throughout this experiment the sheep responded to cooler environments by reducing respiration rate while increasing tidal volume. These responses were similar to those studied in detail by Blaxter and Joyce (1964) using sheep exposed to low temperature, wind and rain.

Shivering intensity during cold exposures

As ambient temperature fell below 24°C sheep began to show signs of shivering, which then increased progressively as the temperature fell to zero. Shivering first appeared as tremors in the fascial muscles of the shoulder. As it increased, the muscles of the rump and flanks became involved, and finally shivering became convulsive and was characterized by large rhythmical contractions of the major muscles. Figure 4 shows oscilloscope traces representing different grades of shivering. At sub-zero temperatures convulsive shivering was accompanied by a continual stamping movement of the feet.

Figure 1 shows the progressive increase in shivering intensity (using EMG estimations) of all groups of sheep. During the first cold exposures the mean ambient temperature at the onset of shivering was +16°C. During second exposures the onset of shivering tended to occur at slightly lower ambient temperatures in all groups of sheep. Although this change was not significant, evidence from visual observations was confirmative. There was no effect of plane of nutrition. Sheep of all groups showed lower intensities of shivering (EMG) on second than on first exposure. When all measurements of shivering intensity between 14.30 hr and 16.00 hr were pooled, a within-animal com-

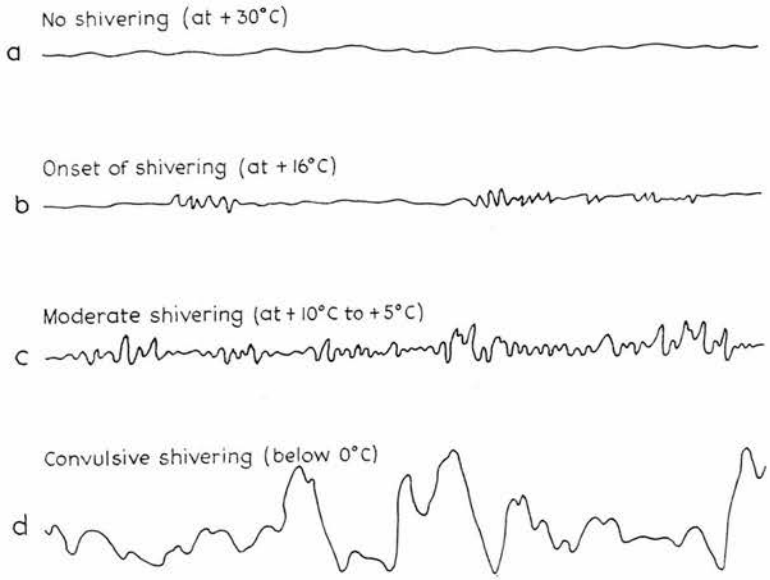


FIG. 4. Typical patterns of shivering at four ambient temperatures during acute cold exposures, as shown by oscilloscope traces.

parison showed the differences in shivering intensity between first and second cold exposures to be highly significant ($P<0{\cdot}001$ in HP8, HP30 and LP30 sheep; $P<0{\cdot}02$ in LP8 sheep). The tendency, apparent in Figure 1, for mean shivering intensity to fall during the later stages of first exposures was associated with the successive removals of the least cold resistant sheep from the chamber (Slee and Sykes, 1967). The most resistant sheep appeared to shiver less than sheep whose body temperature was falling rapidly.

The increased heart rate and decreased shivering intensity, both of which occurred during second exposures, resulted in a changed ratio between heart rate and shivering intensity. This change was most marked and most consistent in the +8 sheep.

Shivering intensity between cold exposures

Sheep kept at +8°C between cold exposures showed persistent shivering, although visual observations suggested some decrease in intensity after several days. Shivering was not observed in sheep kept at +30°C. EMG

recordings were generally confirmatory, but very variable between individuals.

Vasoconstriction, metabolic responses and the critical temperature

Under the usual terms of definition, critical temperature is the highest environmental temperature at which an animal is obliged to increase metabolic rate above the basal level in order to maintain body temperature. It is usually supposed that peripheral vasoconstriction occurs just prior to the metabolic response (e.g. Webster and Blaxter, 1966). Our data show that there was no strict relationship between the ambient temperatures at which heart rates began to increase, vasoconstriction occurred and shivering commenced. In 50 out of 80 individual exposures the increase in heart rate occurred after both ear and foot had vasoconstricted, in 26 cases after vasoconstriction in the ear but before that in the foot, and in 4 cases before either extremity had vasoconstricted. On average, heart rate began to increase at a temperature 3·6°C lower than the mean ambient temperature of vasoconstriction in the feet and ears. The onset of detectable shivering was correspondingly later again, occurring at an average ambient temperature 2·7°C below that at which heart rate increased. In general, the metabolic response (which determines the critical temperature) followed the vasomotor response. Rapid skin cooling due to vasoconstriction could therefore have accelerated the metabolic response, assuming that stimulation of superficial cold receptors is a factor involved in eliciting the metabolic response to cold (see Hardy, 1961). The delay in both vasomotor and metabolic responses occurring after chronic cold exposure suggests that the critical temperature had been lowered by the cold treatment.

Finally, a relationship was found between heart rate and shivering. When all pairs of readings between 10.30 hr and 13.00 hr (+30°C to 0°C) from sheep of all groups were combined, significant correlations were found between shivering intensity and heart rate, $r = +0{\cdot}59$ ($P<0{\cdot}001$) and $r = +0{\cdot}67$ ($P<0{\cdot}001$) on first and second exposure respectively. However, when correlations were done using group means, thereby reducing the effects of individual variation, coefficients lying between +0·91 and +0·98 were obtained for all groups on both first and second exposures. This supports earlier assumptions regarding the relationship between heart rate and metabolic rate.

DISCUSSION

Modifications in physiological responses to cooling have been most intensively studied in man and rodents. In man, for example, they fall into three categories; (i) adaptations associated with ethnic groups living in different thermal environments, (ii) acclimatization caused by exposure outdoors, and (iii) acclimatization caused by low temperature exposure in climate rooms.

Examples of adaptation, both insulative and metabolic, have been observed in Australian Aborigines and Eskimos respectively. The work on adaptation has been reviewed by Hammel (1964). Evidence for insulative changes in acclimatized man is conflicting. Glaser and Shephard (1963) found a progressive increase in hand temperature on successive days of cold exposure,

and Eagan (1963) found a greater resistance to finger cooling in acclimatized men than in controls, indicating *decreased* insulation. Budd (1965) and Budd and Warhaft (1966) found an *increase* in insulation of men in Antarctica, and Davis (1963) found no change in insulation. Work on rodents, e.g. Desmarais and Dugal (1951) and Heroux (1959), has shown a reduction in insulation and an increase in extremity temperatures after acclimatization.

Elevated metabolic rates have been observed in acclimatized men by Scholander, Hammel, Anderson and Løyning (1958), but in no case has summit metabolic response been tested. In rodents, evidence for increases in both basal and summit metabolic rate has been found (Hart, 1963).

In the present work with sheep we have been concerned with the effects of two types of cold exposure: (*a*) acute exposures generally sufficient to induce hypothermia and (*b*) chronic exposures to moderately subcritical temperatures. The main effects of cold exposure were (i) increased resistance to body cooling during acute cold exposure, this being defined as acclimatization, and (ii) other changes associated with acclimatization, viz, increased blood flow to the extremities, increased basal metabolic rate (inferred from change in heart rate), and delayed and reduced shivering responses. It was previously found that increased resistance to cooling was induced mainly by experience of acute cold exposure but possibly also by chronic moderate cold exposure (Slee and Sykes, 1967). Evidence in the present paper shows that the associated responses on the other hand were influenced relatively more by the longer periods of moderate cold exposure. It is not clear how far these associated responses were actually induced during the period of moderate cold exposure and how far they were caused by the preceding acute exposures and merely allowed to persist during the two weeks exposure to +8°C. The latter is somewhat favoured by the fact that the +30 sheep showed elevated heart rates and rectal temperatures (suggesting elevated basal metabolism) on day 4 but not on day 14, and also some delay in foot vasoconstriction during the second acute cold exposure. The assumption then would be that the main acclimatization effect, whether caused by acute cold or chronic cold, could persist through two weeks exposure to +8°C or +30°C; but the associated changes would tend to decay more quickly unless moderate cold exposure (+8°C) was continued.

The sheep at +8°C adopted initially a hunched and stiff posture, which did appear to be relaxed after a few days. Measurements of skin temperature, heart rate and shivering taken at the beginning and end of the two weeks exposure to +8°C (days 4 and 14) showed no evidence for changes in insulation or metabolic rate during this period. However, when the +8 sheep were returned to +30°C, gross changes in response were observed. Heart rates had increased by 40%, and ear and foot temperatures were higher than before first exposure. Rectal temperatures were also elevated (Slee and Sykes, 1967). Similar work on rodents—Gelineo (1934), Cottle and Carlson (1954), Depocas, Hart and Heroux (1957) and Sellers, Scott and Thomas (1954)—has shown basal metabolic rate to be elevated by prolonged cold exposure. It seems probable therefore that an increase in basal metabolic rate had occurred in our sheep. Probably in consequence, the onset of vasoconstriction, onset of shivering and increase in heart rate of the +8 sheep during second exposure, occurred at lower ambient temperatures than during first exposure. This implies a depression of the critical temperature.

In the +8 sheep, during the initial stages of second cold exposure, skin

temperatures remained high whilst rectal temperature was allowed to fall slightly (Slee and Sykes, 1967). At sub-zero temperatures, the +8 sheep also had slightly higher extremity temperatures associated with more pronounced cold vasodilatation on second exposure. The periphery was therefore warmed at the expense of the body core. This response is similar to the hypothermic adaptation found in Andean Indians by Elsner (1963). Carlson, Burns, Holmes and Webb (1953) discussed the concept of changes in the distribution of body heat between the 'shell' and 'core'. Acclimatized animals, by increasing the heat content of the 'shell', particularly the extremities, suffer increased energy loss, but may endure exposure with less discomfort and greater mobility. The occurrence of injuries such as frostbite may also be reduced (Blair, 1951).

The elevated heart rates of the +8 sheep at sub-zero temperatures probably indicate increased metabolic rates, and may in part explain the comparatively greater acclimatization shown by these sheep (Slee and Sykes, 1967), despite their increased heat loss from the extremities.

The changes in peripheral vascularity and heart rate were confined largely to the +8 sheep, but improvement in resistance to body cooling was shown by almost all sheep, irrespective of whether kept at +8°C or +30°C between acute cold exposures. Similarly, the reduced shivering intensity during second exposure occurred in all groups of sheep. Davis and Johnston (1961), Davis (1963) and Scholander *et al.* (1958) also demonstrated decreased shivering after acclimatization in men. Cottle and Carlson (1956), Hart, Heroux and Depocas (1956), Heroux, Hart and Depocas (1956) and Sellers, Scott and Thomas (1954) showed that, in acclimatized rodents, heat production could be increased without shivering. While shivering is more efficient than work (voluntary muscle activity) as a source of heat production, it probably causes a reduction in body insulation due to: (i) increased peripheral blood flow, (ii) increased convective heat losses associated with skin tremors and (iii) the superficial site of thermogenesis. Muscle cooling may also reduce the efficiency of shivering under severe cold exposure. A method of heat production nearer the body core and compatible with maximal insulation, should be more efficient. It seems possible that, in our sheep, the apparent reduction in shivering intensity after low temperature exposure was associated with some alteration in the site and manner of heat production which enhanced the ability to resist body cooling. Such an explanation is supported by the change in ratio between heart rate and shivering intensity found during second exposure. This presumably indicates an increase in metabolic capability coupled with a decrease in shivering thermogenesis. However, in view of the large improvement in resistance to cooling compared to the fairly small reduction in shivering intensity, it seems likely that other factors also contributed to the production of acclimatization.

Summarizing, therefore, there was evidence for increases in basal metabolism and in summit metabolic capability after chronic moderate cold exposure. There were also changes in other physiological responses to cold, resulting in an altered distribution of body heat. Following acute cold exposure on the other hand, there appeared to be changes in the efficiency of production and utilization of body heat, possibly through the development of non-shivering thermogenesis. Presumably these factors were involved in the improved resistance to hypothermia shown previously (Slee and Sykes, 1967). Amongst individual sheep, there was no clear relationship between the degree of

improvement in resistance to hypothermia and the accompanying physiological changes. Nevertheless, the physiological responses were remarkably uniform, in that within treatment groups all animals tended to behave alike.

The apparently different effects of acute cold exposure alone (as experienced by the +30 sheep) and those of chronic moderate cold exposure, raise the question of how far these different responses are part of the same process. One possible explanation is that they comprise different aspects of acclimatization and have slightly different properties. For example, the effects of cold exposure upon basal metabolism and peripheral blood flow may be relatively ephemeral and easily lost unless the ambient temperature remains low, whereas increased resistance to cooling, perhaps mediated by the development of non-shivering thermogenesis, might be a relatively indelible response which could be maintained during two weeks at a thermoneutral temperature.

It should be emphasised that the present findings from the cold exposure of shorn sheep do not necessarily imply that fleece-covered sheep subjected to equivalent intensities of cold would respond similarly. For example, with respect to respiration rate, Bligh (1963) has shown how shearing, with consequent exposure of peripheral cold receptors, can grossly alter the short-term responses of sheep to changes in ambient temperature. Also Webster (1966) found metabolic and rectal temperature responses during cold exposure to be essentially different in sheep with long and short fleeces.

However, in our experiments, all the sheep were shorn and all were subjected to severe cold exposures sufficient, probably, to elicit maximum metabolic response. Some of the sheep also received chronic moderate cold treatment. As a result, a number of physiological changes were induced which persisted for varying periods of time after the cold stimuli were removed. These changes were associated with a greatly increased resistance to hypothermia, i.e. acclimatization. The extent to which each type of cold treatment was responsible for different physiological responses, and the precise role of these physiological changes in inducing acclimatization is not entirely clear.

SUMMARY

Closely shorn Scottish Blackface female sheep aged 9–14 months, half on high plane and half on low plane nutrition, were subjected, in climate chambers, to two short acute cold exposures down to −20°C. The acute exposures were separated by two weeks chronic exposure to a moderately subcritical temperature (+8°C) or to a thermoneutral temperature (+30°C). Most of the sheep showed a greater resistance to body cooling at the second acute exposure (Slee and Sykes, 1967). This increased resistance to hypothermia, defined as acclimatization, was apparently influenced more by acute than by chronic cold exposure. The present paper deals with changes in skin temperature, heart rate, shivering intensity and skinfold thickness which also resulted from cold exposure, and accompanied acclimatization.

After acute cold exposure followed by chronic exposure to +8°C the following changes in these parameters were observed:

1. Extremity skin temperatures and heart rates were consistently increased at thermoneutral ambient temperatures.

2. Vasoconstriction of the extremities and increased heart rate, both of which normally occur during the early stages of cold exposure, were delayed.

3. Heart rates at sub-zero ambient temperatures were increased.

4. Cold-induced vasodilatation at sub-zero ambient temperatures was increased.

After acute cold treatment alone the intensity of shivering during the second acute exposure was reduced. Also the onset of foot vasoconstriction was slightly delayed.

A highly significant relationship was observed between shivering intensity and heart rate during cold exposure.

Plane of nutrition had less effect on the physiological responses to cooling than did previous cold experience.

It was suggested in discussion that the physiological responses associated with acclimatization were: elevated basal metabolic rate, delayed onset of vasoconstriction and delayed metabolic response to cold, and consequent lowering of the critical temperature. Summit metabolism was also increased and shivering intensity reduced during acute cold exposure. Some of these responses could have resulted from either acute or chronic moderate cold exposure. However their persistence, once induced, appeared to depend upon continued exposure to moderate cold.

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